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TOO WET FOR AQUATIC PLANTS?

FLORISTIC COMPOSITION AND PHYTODIVERSITY IN THE WETLANDS ALONG THE BASE OF THE BOLIVIAN ANDES

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ABSTRACT. An investigation of the vascular plant flora of the wetlands in the Chapare, an extremely high-precipitation region along the base of the Bolivian Andes, was undertaken from 1994 to 1996. One hundred fifty-one species in 52 families and 107 genera were identified as occurring in the region's wetlands. In contrast to the terrestrial flora of the Chapare and of other regions in the Andean forelands, Chapare wetlands were found to be characteristically species-poor (5–49 species). Nevertheless, the Chapare wetland flora contained a number of rare or noteworthy species, and represented the southern distributional limit for a number of taxa. The diversity of Chapare "wetland species" (i.e., species considered to be strongly associated with Neotropical wetlands) was low relative to other South American lowland regions when considered in terms of total number of species and from species-area curves. A regional trend toward fewer wetland species with increased precipitation was apparent; however, data supporting this relationship were inconclusive. Despite low floristic similarities (Sørensen's Index) between study sites, the majority of the Chapare study sites were closely situated in an ordination by Detrended Correspondence Analysis (DCA) of the floras of 46 wetlands distributed throughout Bolivia. At the regional scale, floristic similarities with other regions considered in this study were relatively low. As might be expected, an ordination of the regional data indicated that the Chapare wetland flora was most strongly associated with the other lowland Bolivian regions, while the most geographically distant regions were also the furthest removed in ordination space.

Key Words: Neotropics, Bolivia, Chapare, wetlands, aquatic plants, phytodiversity

The region along the base of the Cordillera Oriental (Eastern Range) of the Bolivian Andes in the Department of Cochabamba is colloquially referred to as the *Chapare*. At times, the Andean slopes are also included in the delineation of the Chapare (e.g., Guyot and Watson 1994; Solomon 1989), but the name is most often used solely in reference to the lowlands, a usage that is also applied here. The Chapare (Figure 1) occupies the transition between the Andes and the extensive floodplain that extends northwards through the Department of Beni and eastwards to the Brazilian Shield. The largest part of this floodplain, the Beni basin, is characteristically quite level and occupies elevations between 150–250 m

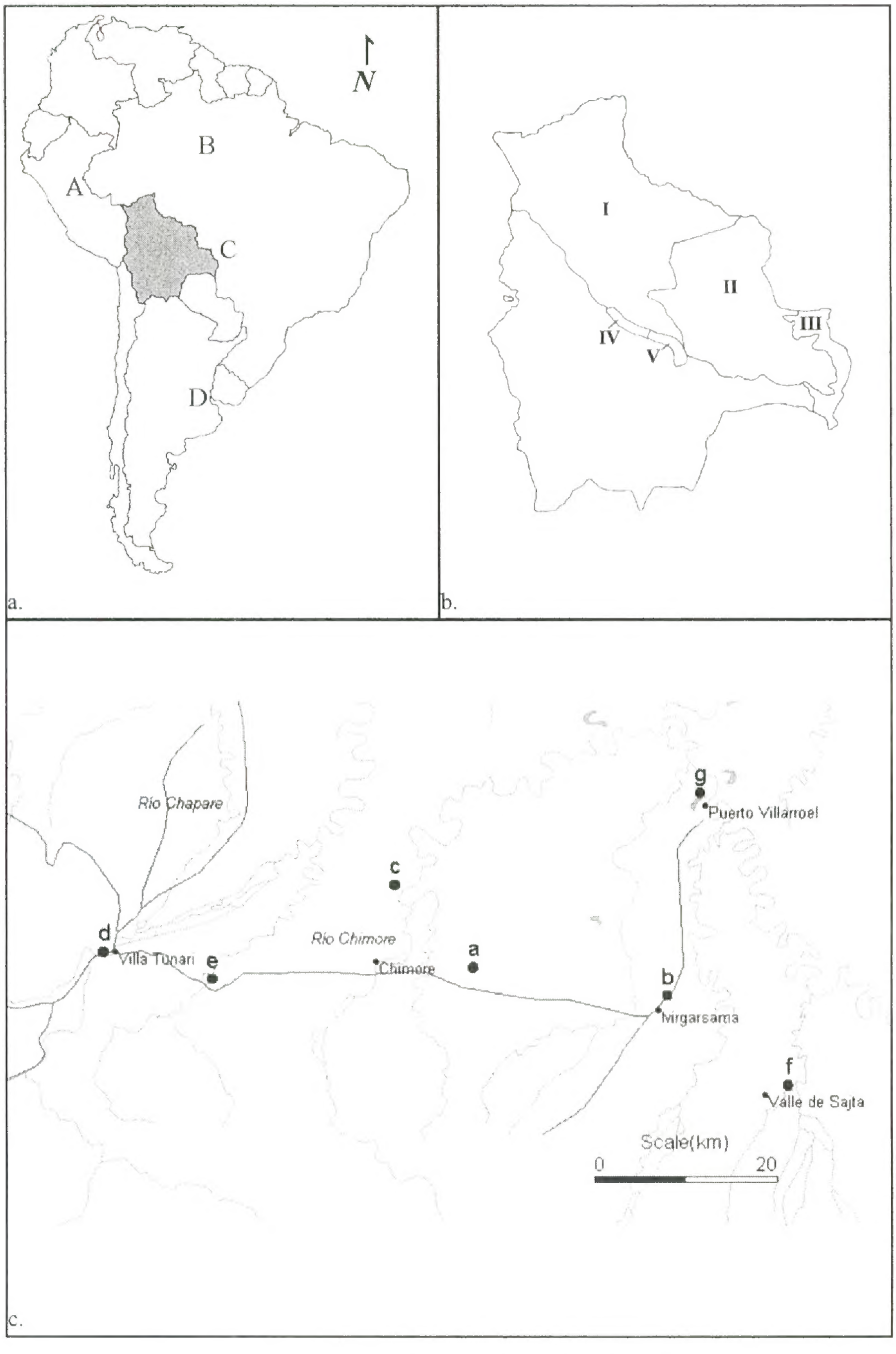

Figure 1. Study site locations. a. South America, with approximate centers of extra-Bolivian Operational Geographic Units (OGUs): A. Lowland Amazonian Peru; B. Central Amazonia; C. Brazilian portion of the Gran Pantanal de Mato Grosso; D. Río Paraná Delta. Bolivia occupies the shaded portion in the center of the continent. b. Bolivia, with approximate delineation of the Bolivian OGUs: I. White-water

(Killeen et al. 1993; Plafker 1964). Topography in the Chapare is more variable, with low hills creating a dissected relief. Although the Chapare region includes territory from three provinces (Chapare, Tiraque, and Carrasco) the colloquial name for the region is quite functional, circumscribing an area characterized by high rainfall, high temperatures, low elevations, and (previously) extensive tracts of rainforest. Although the precise geographic limits are not clearly defined, the Chapare has an area of approximately 3000 (Henkel 1995) to 4000 km^2 (determined from maps using the ''cut and weigh method,'' cf. Lind 1985).

The Chapare is situated in an ''inside corner'' of the Andes, formed by a change from an approximately southwest to northeast orientation of the mountains to a more eastern bearing. This region and the adjacent Andean slopes receive the highest amount of rainfall in Bolivia. Maximum mean annual precipitation in the Chapare reaches an estimated 4900 mm/yr, with a maximum hydrologic year of 6900 mm (Morris et al. 1983). Rainfall is even greater in the lower Andean slopes just above the Chapare, where mean annual precipitation is estimated to reach 6000 (Moraes and Beck 1992) to 7000 mm/yr (Guyot and Watson 1994). Rainfall decreases northwards away from the mountains and eastwards toward the City of Santa Cruz (Morris et al. 1983). Thus, in the approximately 70 km between the two most disjunct Chapare study sites (see Materials and Methods) mean annual precipitation ranged from about 2500 mm to $>$ 4500 mm (estimated from isohyets presented in Morris et al. 1983). Despite abundant precipitation, the region still experiences a few months of low rainfall (roughly, June to August), such that many of the area's small ponds and roadside ditches dry out completely. Mean monthly temperatures range from 20° to 38°C (Henkel 1995), with a mean annual temperature of 21.8° (Maldonado et al. 1996) to 25°C (Killeen et al. 1993). Temperatures in the region always remain above 0°C.

The slopes of the Cordillera Oriental are precipitous, with the transition between montane peaks ($>$ 4500 m) and the lowlands occurring over a short distance (ca. 30–40 km, *linea recta*). The slopes above the Chapare are characterized by deposits of sedimentary rocks that consist primarily of shales and may be greater than 200 m in thickness (Morris et al. 1983).

←

Floodplain; II. Chiquitanía; III. Bolivian portion of the Gran Pantanal de Mato Grosso; IV. Chapare; V. Andean Piedmont. c. Location of the Chapare (Bolivia) study sites: a. Mariposa Wetland; b. Ivirgarsama Marsh; c. Senda F Wetland; d. Villa Tunari Pond; e. Sinahota Pond; f. Valle de Sajta Curichi; g. Puerto Villarroel Laguna.

These substrata and their derived soils are unstable and tend to erode rapidly when stripped of vegetation (Morris et al. 1983); rates of erosion are extremely variable, ranging from an estimated 1000–20,000 t/km^2/yr (Guyot and Watson 1994). At the base of the mountains, the shales are overlain by deposited alluvial materials. These deposits are generally arrayed sequentially from coarse materials at the foothills to finer-grained sediments away from the mountains (Morris et al. 1983).

The rivers draining the steep Andean slopes arrive at the Chapare with great force and are extremely dynamic upon reaching the easily erodible soils. Erosion and sedimentation occur rapidly (Morris et al. 1983), with lateral channel migrations a constant feature of the Chapare's rivers. Salo et al. (1986) analyzed channel dynamics in Peruvian Amazonia by comparing aerial photographs from 1962–63 with a 1976 Landsat (satellite) image. They estimated that for their area of study in lowland Peru the mean lateral erosion rate of meander bends during this period was 12 m/yr (Salo et al. 1986). It seems reasonable that channel migration in the Chapare rivers could be of a similar magnitude.

The rivers of the Beni basin are characteristically very turbid (Guyot and Watson 1994), corresponding to white-water rivers (*sensu* Sioli 1975). On the floodplain, the rivers are an opaque brown from their large load of suspended fine particles; however, river water in the Chapare is generally much more transparent. This phenomenon presumably occurs because the rivers and streams that drain the Andean slopes are generally clear and only carry large amounts of sediments when the vegetative cover, which protects the weathered substratum, is subjected to landslides and other large-scale disturbances (cf. Sioli 1984).

Historically, the Chapare's terrestrial vegetation was dominated by tall forest, characterized by high diversity (Killeen et al. 1993). However, during the 1960s and '70s the government advanced colonization of the region, constructing roads to and within the Chapare and apportioning 202,000 ha of land for new colonists (Henkel 1995). Logging has been extensive and large portions of the region have been cleared for agriculture, with approximately 80% of the land dedicated to the cultivation of coca (*Erythroxylum coca*) and the remaining 20% to other crops. Consequently, the greatest part of the Chapare's remaining forested habitats are secondary forest.

There have been few limnological investigations of the Chapare's aquatic habitats, and references to the aquatic flora are nearly nonexistent. Limnological studies were undertaken by Barra et al. (1990), Cadima (1990), and Maldonado et al. (1996). Of these, the sole reference to the vascular flora was from Maldonado et al., who listed the macrophytes

Table 1. Study sites of the Chapare region (Bolivia), with elevation, approximate area, number of species encountered, approximate location, and dates visited.

Study Site Name	Elev. (m)	Area (ha)	Spp.	Location	Dates Visited
Mariposa Wetland	220	1.5	49	17°01′S, 65°02′W	11/27/94; 3/5/95; 6/8/95; 11/1/96
Ivirgarsama Marsh	200	0.7	44	17°01′S, 64°50′W	2/23–24/96; 5/10/96; 10/27/96
Senda F Wetland	200	0.2	19	16°52′S, 65°08′W	6/1/94; 11/11/94; 3/4/95
Villa Tunari Pond	300	0.3	11	17°01′S, 65°26′W	11/12/94; 3/5/95; 6/8/95
Sinahota Pond	240	0.15	9	17°00′S, 65°18′W	11/12/94; 6/8/95
Valle de Sajta Curichi	220	0.2	6	17°07′S, 64°43′W	3/20/95
Puerto Villarroel Laguna	200	30.0	5	16°49′S, 64°48′W	3/19/95; 11/1/96

encountered in a series of lakes on the Río Ichilo floodplain. Additional information comes from Jiménez (1984), who listed various wetland species in his account of the flora of the Department of Cochabamba.

In the present study, I undertook a botanical survey of the wetlands of the Chapare as a portion of a larger study of the wetlands of Bolivia (Ritter 2000). My specific objectives were as follows: 1) to prepare a provisional checklist of the vascular plant species associated with Chapare wetland habitats; 2) to identify rare or noteworthy species from these habitats; 3) to estimate the range of site-level vascular plant species richness; 4) to compare species richness in the Chapare wetland flora to lowland regions in Bolivia and other South American countries; and 5) to examine floristic similarities among the Chapare wetland flora and these regions. To these ends, the flora of the Chapare wetlands is listed and noteworthy species are discussed. Comparisons of species richness and floristic similarity are made between study sites. At the regional level, comparisons are made among the Chapare wetland flora and seven lowland regions in Amazonia and extra-Amazonian South America.

MATERIALS AND METHODS

Study sites. Within the Chapare, seven wetland systems were established as study sites (Table 1; Figure 1). Although field research was concentrated on these systems, additional botanical collecting was undertaken in a variety of wetland types (e.g., small marshes, streams,

rivers, oxbow lakes, strand lakes, and inundated roadside ditches). Brief descriptions of the study sites follow.

1. Mariposa Wetland.

The Mariposa Wetland was located alongside the highway from the Chapare to Santa Cruz, approximately 1.5 km east of the community of Mariposa. The system consisted of two small (< 0.3 ha) ponds fringed with a strip of marshy habitat. The ponds occupied shallow depressions (ca. 2 m deep) that were created when fill for an adjacent highway was excavated from the site. The marsh was situated between the ponds and the highway and was essentially a wide (ca. 50 m) section of the "borrow canals" that typically flanked the highway and other roads in the region. Although these canals extend for many kilometers, investigations of the Mariposa "system" were limited to an approximately 200 m long section of marsh, centered on the two ponds. A small, seasonal stream delineated the western edge of the study site. Total study site area was approximately 0.8 ha.

In contrast to many similar small bodies of water in the Chapare, the ponds contained water throughout the year, suggesting that they received some subsurface water inflow. During the dry season, standing water disappeared from most areas of the marsh; soil conditions varied from fairly dry to saturated during this period. Although this system undoubtedly received substantial inputs of runoff from adjacent uplands during the rainy season, there were no large rivers near the site. Thus, the system did not appear to receive the periodic influxes of water-borne sediment that were characteristic of many of the Chapare's aquatic habitats.

2. Ivirgarsama Marsh.

The Ivirgarsama Marsh was located alongside the unpaved road that connected the highway to Santa Cruz with the town of Puerto Villarroel. The system was composed of a small (ca. 0.2 ha) shallow pond with an adjoining (ca. 0.5 ha) marshy area in the area between the pond and the road. Smaller sections of marsh also occurred along the other edges of the pond. A narrow stream flowed through the system, entering the pond at one end and discharging through the marsh at the far end of the system. As with the Mariposa Wetland, the marsh was essentially a widening of a typical roadside borrow canal, however the pond at the Ivirgarsama Marsh appeared to be of natural origin. The Ivirgarsama Marsh was unique among the Chapare study sites because of the well-developed floating mats of vegetation present along the edges of the pond.

3. Senda F Wetland.

The Senda F Wetland was located between the town of Chimoré and the Río Chapare. The system was situated adjacent to an unpaved road and was contiguous with the borrow canals that flanked the road. A small stream flowed into the southeast corner of the marsh, and a number of small, fairly deep pools were present. Hence, habitat heterogeneity was much higher than was typical for the region's roadside canals. The area surveyed was approximately 80 m long with a maximum width of about 15 m on either side of the road. Water levels at the site fluctuated seasonally and standing water was absent from parts of the marsh during the driest portions of the year.

4. Villa Tunari Pond.

The Villa Tunari Pond was a small pond located alongside the Cochabamba-Santa Cruz highway, approximately 4 km east of the town of Villa Tunari. As it was situated near to the start of the ascent of the Cordillera Oriental (Eastern Range) of the Andes, the system occupied a slightly higher elevation (300 m) than the other Chapare sites. During the dry season, the pond's surface covered an area of about 0.3 ha; during the rainy season, large portions of the upland areas adjacent to the pond became shallowly inundated and the limits of the "system" were indistinct. Maximum depth during the rainy season was on the order of 2.0–2.5 m; water levels dropped significantly during the dry season. Although the basin was never observed to be entirely without standing water, it seems likely that this might occur during dry years.

5. Sinahota Pond.

The Sinahota Pond was another small (approximately 0.15 ha) seasonal pond situated alongside the Cochabamba-Santa Cruz highway, approximately 2 km west of the town of Sinahota. Maximum depth during the rainy season was about 2.0 m; during the dry season the system dried out completely. The basin was fairly steep-sided and, in contrast to the Villa Tunari Pond, inundation did not appear to extend to the surrounding areas during typical high water stages.

6. Valle de Sajta Curichi.

In the Bolivian lowlands, a "curichi" is a system that occupies a section of a former river channel, and which normally does not dry-down completely during the dry season (Beck 1984). The Valle de Sajta Curichi consisted of two small ponds separated by a narrow (10 m) strip of land. The ponds originally comprised a section of a river channel—most likely

the nearby Río Zabala—and developed into their present form after being stranded due to channel migration. The ponds appeared to be connected by a subterranean passage and the system was said to contain water year-round.

7. Puerto Villarroel Laguna.

The Puerto Villarroel Laguna, a large curichi, was the largest and deepest of the Chapare study sites. Despite being located in a region characterized by "white-water," the system's water was stained dark from organic acids. Maximum depth was difficult to determine, but appeared to be at least 4 m. The lake's area as estimated using the cut and weigh method (Lind 1985) on a 1:100,000 scale topographical map, was found to occupy 70 ha; however, during visits to the site the area was visually estimated at about 15 ha. As a compromise, 30 ha. was selected as a rough approximation of the system's size.

Vegetation sampling. Sampling focused on compiling comprehensive site floras. As noted, the study sites were fairly limited in size (Table 1); it was possible to survey each site in its entirety. Fieldwork was conducted intermittently from June 1994 to November 1996. Sites received multiple visits (Table 1) whenever possible in order to view the systems under different hydrologic conditions and thus to maximize the number of species encountered. Preferably, fieldwork was scheduled so that sites were visited during both the wet and dry seasons, but due to various constraints this was not always possible.

Voucher specimens were made of all species observed at each site and, with one exception, were deposited in the Herbario Forestal (BOLV; Cochabamba) and the University of New Hampshire's Hodgdon Herbarium (NHA). When available, duplicates were deposited at the Herbario Nacional de Bolivia (LPB; La Paz), the herbarium of the Museo de Historia Natural "Noel Kempff Mercado" (USZ; Santa Cruz), and the Missouri Botanical Garden herbarium (MO). A checklist, including life-form and species abundances at each site, is presented as an Appendix.

Floristic comparisons. A regional checklist of wetland species was compiled from the study sites and augmented by data from general collecting in the Chapare, from the literature, and from exsiccatae listed in the Missouri Botanical Garden database, TROPICOS. Published sources used to augment the checklist were Maldonado et al. (1996), which was incorporated in its entirety, and Jiménez (1984), which was reviewed for species collected from the Chapare.

Table 2. Operational Geographic Units (OGUs) utilized in this study, with estimated total area, number of wetland species, and floristic similarity (Sørensen's Index) between the OGU and the Chapare. Detailed descriptions of the OGUs and an account of the sources used in compiling the floras are given in Ritter (2000).

OGU	Approximate Area (km^2)	No. of Species	Floristic Similarity
Chapare	4000	113	–
Andean Piedmont	5000	244	33.6
White-water Floodplain	325,000	464	31.5
Chiquitanía	190,000	541	28.4
Gran Pantanal (Bolivia and Brazil)	140,000	451	23.4
Central Amazonia (Brazil)	70,700	429	32.8
Lowland Amazonian Peru	533,100	255	28.8
Río Paraná Delta (Argentina)	23,700	297	10.7

Floristic relationships were analyzed at two scales: 1) among study sites and, 2) among regions (mesoregional scale *sensu* McLaughlin 1994). Regional comparisons were made among the flora of the Chapare and the following OGUs (Operational Geographical Unit, cf. Crovello 1981): Central Amazonia (Brazil), Lowland Amazonian Peru, the Río Paraná Delta region (Argentina), the Gran Pantanal de Mato Grosso (Bolivia and Brazil), and three additional areas of lowland Bolivia (the White-water Floodplain, Chiquitanía, and Andean Piedmont regions). For each OGU, estimated total area, total wetland species, and calculated floristic similarities are presented in Table 2. It should be noted that the total number of wetland species included for the Chapare in regional comparisons is less than the number of species listed in the Appendix, as species lacking complete identifications and species not considered to be strongly associated with wetlands were excluded from regional floristic comparisons. Salient characteristics of the OGUs are presented where warranted; detailed descriptions, and an account of the sources used to compile OGU floras are given in Ritter (2000).

Ascription of ``wetland species.'' In order to undertake regional-scale comparisons, a checklist of wetland species (Ritter, unpubl. database) was used to determine species presence in each OGU. A complete account of the sources used in compiling the checklist and a discussion of the criteria used in the ascription of species is presented in Ritter (2000).

Data analysis. Degrees of floristic similarity among OGUs were analyzed using Sørensen's Index (Magurran 1988):

$$S = 2j \div (a + b)$$

where a is the total number of species in OGU 1, b the total number of species in OGU 2, and j the number of species present in both OGU 1 and OGU 2.

As with most similarity indices, Sørensen's Index gives equal weight to all species in calculating floristic similarity. However, shared rare or uncommon species in a pair of OGUs can also serve as valid indicators of floristic similarity (Simberloff and Connor 1979). In order to assess the relative contribution of these species to overall floristic similarity, the frequencies of "species classes" (e.g., species present in all OGUs, species restricted to 2 OGUs, etc.) were graphed. This analysis was not conducted among all OGUs; rather it was restricted solely to comparisons between the Chapare flora and the other OGUs. Because floristic similarities (Sørensen's Index) between the Río Paraná Delta region and all other OGUs were uniformly low, this OGU was excluded from this analysis.

In order to express floristic relationships among all OGUs simultaneously, data were organized into a binary matrix of OGUs versus species (recorded as presence-absence values) and were ordinated using Detrended Correspondence Analysis (DCA; Hill and Gauch 1980). Ordinations were conducted using the software package, PC-ORD (MjM Software, Gleneden Beach, OR).

RESULTS

Vegetation description. One hundred fifty-one species, in 52 families and 107 genera, were identified as being associated with Chapare wetlands (Appendix). The Poaceae (14 genera, 25 spp.) and Cyperaceae (8 genera, 17 spp.) were the best-represented families; *Panicum* (Poaceae, 9 spp.) and *Ludwigia* (Onagraceae, 7 spp.) were the best-represented genera.

Biodiversity. The number of species encountered at the individual sites varied widely (5–49 spp.; Table 1), and was not consistently correlated with area. For example, the largest site (the Puerto Villarroel Laguna, 30 ha) possessed the fewest species (5), and the second largest site (the Mariposa Wetland, 1.5 ha) the greatest number of species (49). In order to compare richness in the Chapare sites with wetlands from other

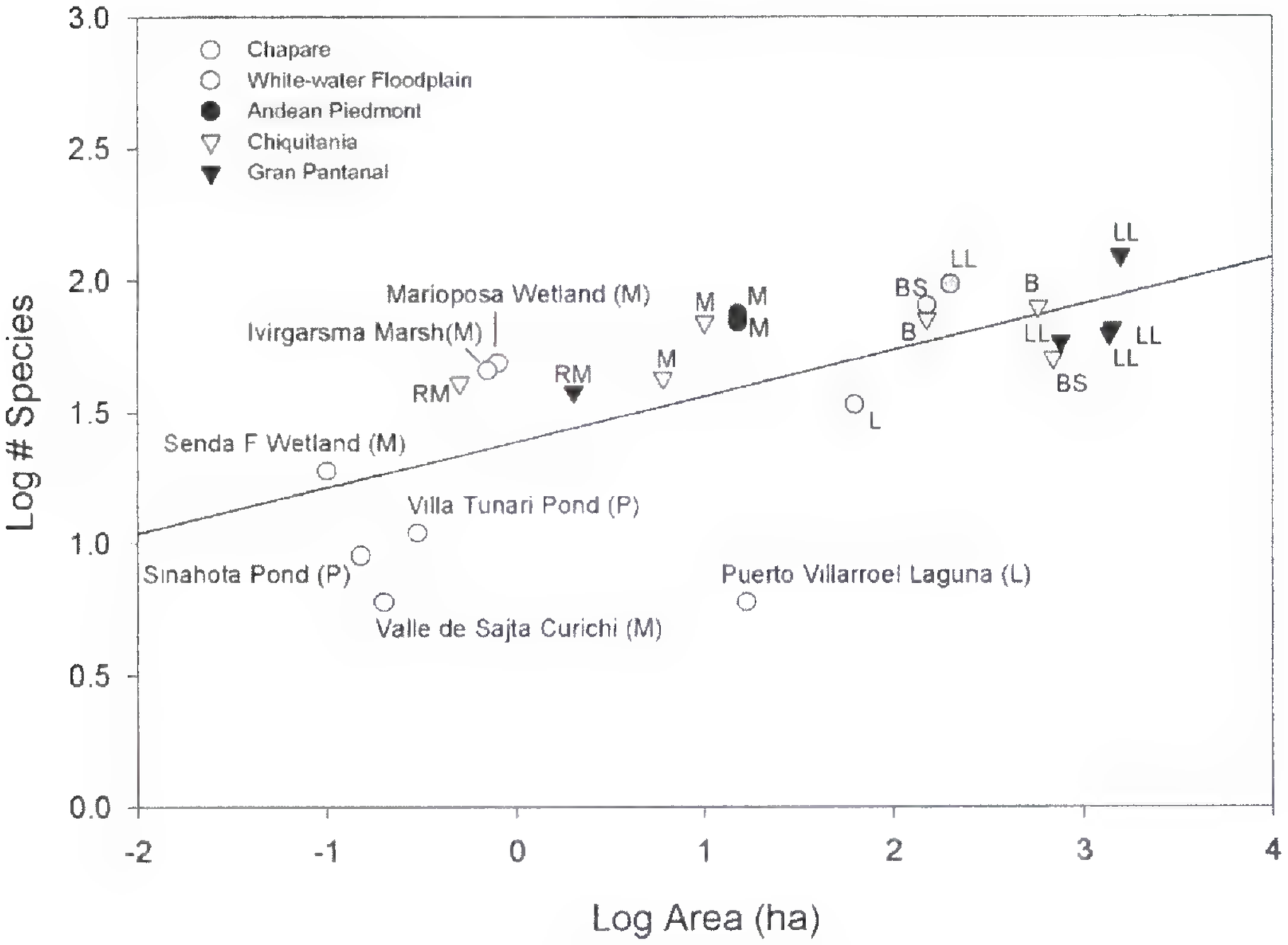

Figure 2. Species-area curve plotted from data from 23 lowland Bolivian wetlands (Ritter 2000), with the Chapare (Bolivia) study sites identified by name. Wetland types: B, bahía; BS, basin swamp; L, small lake (< 500 ha); LL, large lake (> 500 ha); M, marsh; P, pond; RM, riparian marsh. Linear regression: log S − 1.39 + 0.17 log A; $r^2 = 0.44$.

Bolivian lowland regions, a species-area curve (Figure 2) was plotted from the Chapare data augmented with data from an additional 16 Bolivian lowland wetland systems (Ritter 2000). Study sites situated above the regression line were considered to be relatively species-rich, whereas those below the line were considered to be relatively species-poor. The Chapare sites could generally be characterized as species-poor, as four of the seven systems were located well below the regression line. Of the remaining systems, one was located just above the regression line, and two were situated well above the line.

At the regional level, wetland floras ranged from 113–541 species, with the Chapare possessing the poorest and the Chiquitanía the richest floras (Table 2). In order to establish a point of reference for comparing diversity among OGUs, a species-area curve (Figure 3) was plotted using cumulative species (wetland species) and area (total regional area) for the countries of the Neotropics and Mexico (Ritter 2000). This curve was considered to represent the general trend for wetland species richness throughout the Neotropics. Discrete species-area data from the Chapare

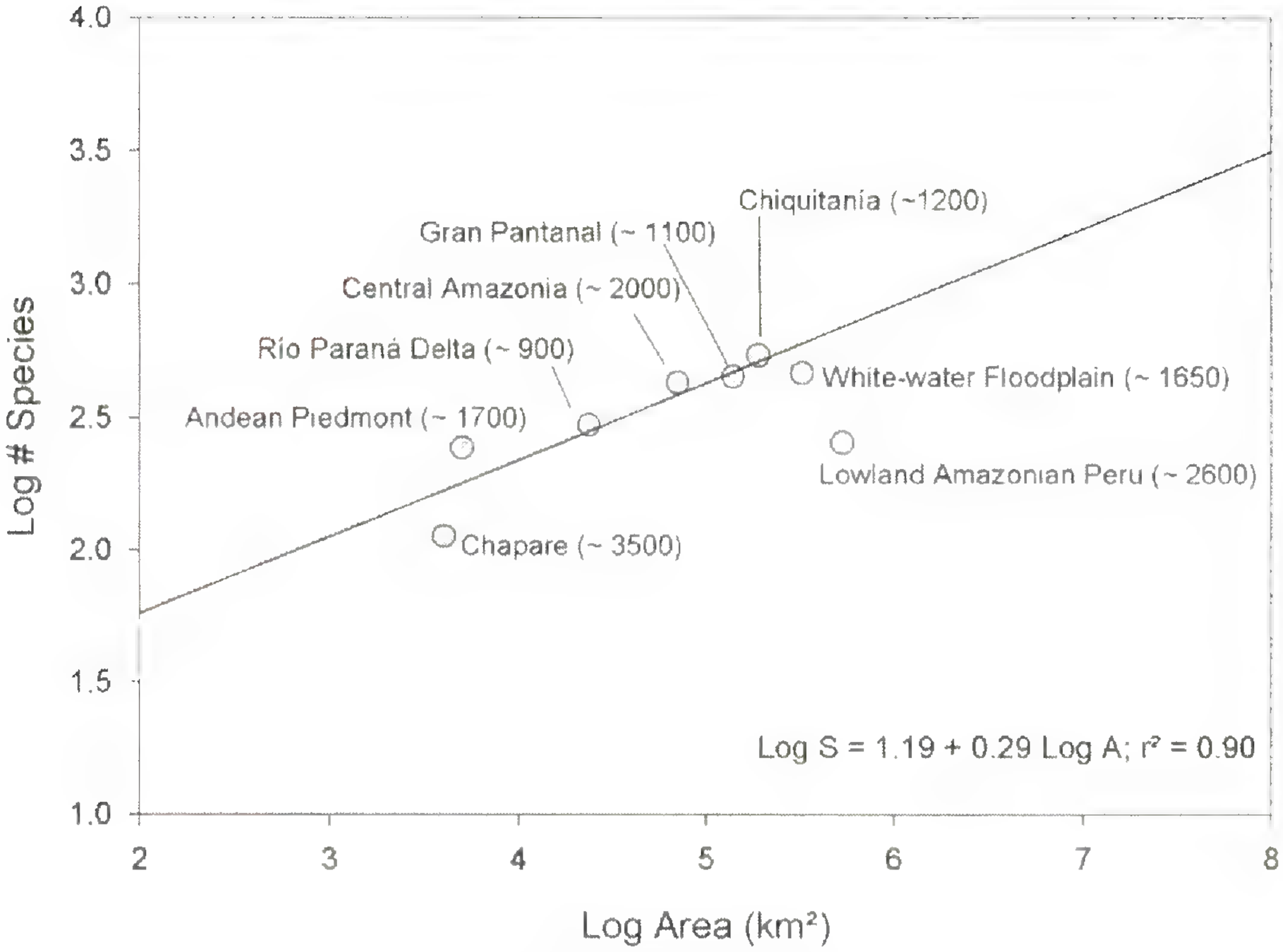

Figure 3. Species diversity of the Operational Geographic Units considered in comparisons with the Chapare (Bolivia) wetland flora. Diversity is relative to a regression line fitted to a species-area curve plotted from cumulative species-area data from the Neotropical countries, including all of Mexico (see Ritter 2000). Values in parentheses indicate estimated mean annual precipitation (mm/yr). Linear regression: log S = 1.19 + 0.29 log A; $r^2 = 0.90$.

and the other OGUs considered here were added to the plot. It was evident that the Chapare could, indeed, be considered species-poor, as it was situated well below the regression line. Other species-poor OGUs were Lowland Amazonian Peru and the White-water Floodplain. By contrast, the Andean Piedmont region, which is contiguous with the Chapare, constituted the richest OGU.

Floristic similarities. Floristic similarities (Sørensen's Index) between study sites were quite variable, ranging from 0–43.0%. In general, floristic similarities were low, with all but three pairs of sites having similarities below 20%. Despite the generally low floristic similarities, five of the seven Chapare study sites were closely situated in ordination space in an ordination (DCA) of the 46 Bolivian study sites (Figure 4).

At the regional level, the Chapare showed the least floristic similarity (Sørensen's Index) to the Río Paraná Delta region (10.7%; Table 2);

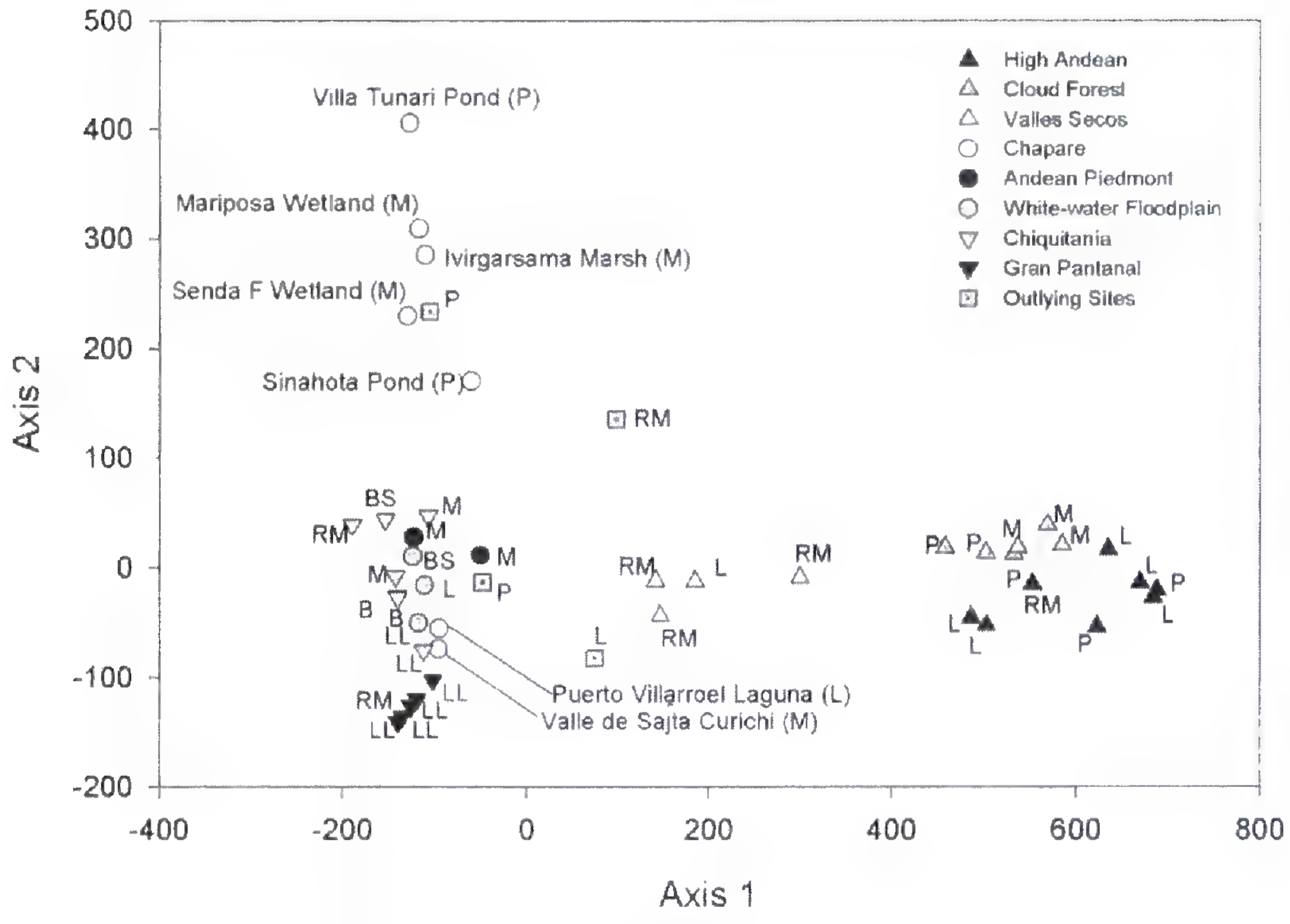

Figure 4. Ordination by Detrended Correspondence Analysis (DCA) of 46 Bolivian study sites. The seven Chapare study sites are identified by name. Key to wetland types: B, bahía; BS, basin swamp; L, small lake (< 500 ha); LL, large lake (> 500 ha); M, marsh; P, pond; RM, riparian marsh. Data from Ritter (2000a).

however, the latter showed few floristic affinities to any of the OGUs (10.7–27.8%). Floristic similarities between the Chapare and the remaining OGUs showed little variability, ranging from 23.4–33.6%. The Chapare was most similar to the Andean Piedmont (33.6%), but this was scarcely higher than the similarities between the Chapare and Lowland Amazonian Peru (32.8%) and White-water Floodplain (31.5%) regions.

An ordination of the regions by DCA (Figure 5) suggested that the floristic relationships were more complex than suggested by Sørensen's Index. The Chapare and the remaining lowland Bolivian OGUs were grouped in fairly close proximity in ordination space. The extra-Bolivian Amazonian OGUs (Lowland Amazonian Peru and Central Amazonia) occupied positions that were disjunct from this grouping. The Río Paraná Delta region formed the endpoint of the first axis, occupying a position far removed from all other OGUs.

A graphical representation of the distribution of species frequency "classes" (Figure 6), demonstrated that the relative contribution of the different classes to floristic similarities was quite variable. In order to facilitate discussion of these relationships, descriptive names were

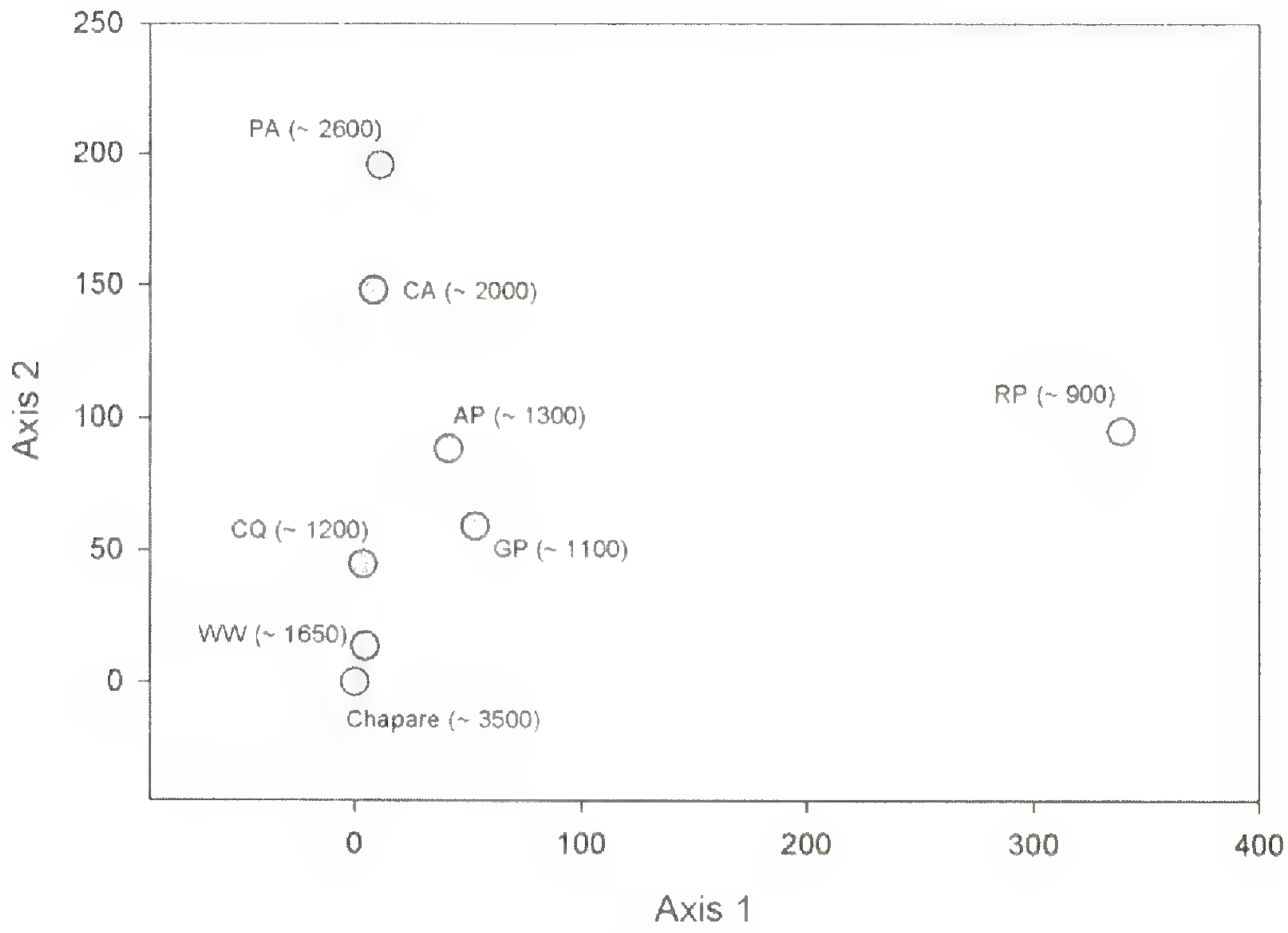

Figure 5. Ordination of the Operational Geographic Units (OGUs) by Detrended Correspondence Analysis (DCA). OGUs: AP, Andean Piedmont; CA, Central Amazonia; CQ, Chiquitanía; GP, Gran Pantanal; PA, Lowland Amazonian Peru; RP, Río Paraná Delta; WW, White-water Floodplain. Values in parentheses indicate estimated mean annual precipitation (mm/yr).

assigned to the four "classes" of species: 1) "ubiquitous," present in all OGUs; 2) "widely distributed," present in 6 OGUs; 3) "intermittent," present in 4–5 OGUs; and 4) "rarely shared," restricted to 2–3 OGUs. It should be noted that these labels were not intended to represent actual species distributions; rather, they refer to species distributions within this particular set of OGUs. In all cases, ubiquitous and widely shared species contributed the greatest amount to floristic similarity (52.7–79.2%), with intermittent species accounting for the greatest portion (18.8–39.8%) of the remaining similarity. In all cases, rarely shared species contributed relatively little (1.9–13.4%) to overall floristic similarity.

DISCUSSION

Vegetation description. The Chapare wetlands were distinct from wetlands of other South American lowlands regions, both in floristic composition and structure. Floating vegetation mats, a typical feature of lowland Neotropical wetlands (e.g., Junk 1970, 1983), were conspicuously absent from the majority of the Chapare study sites. Exceptions

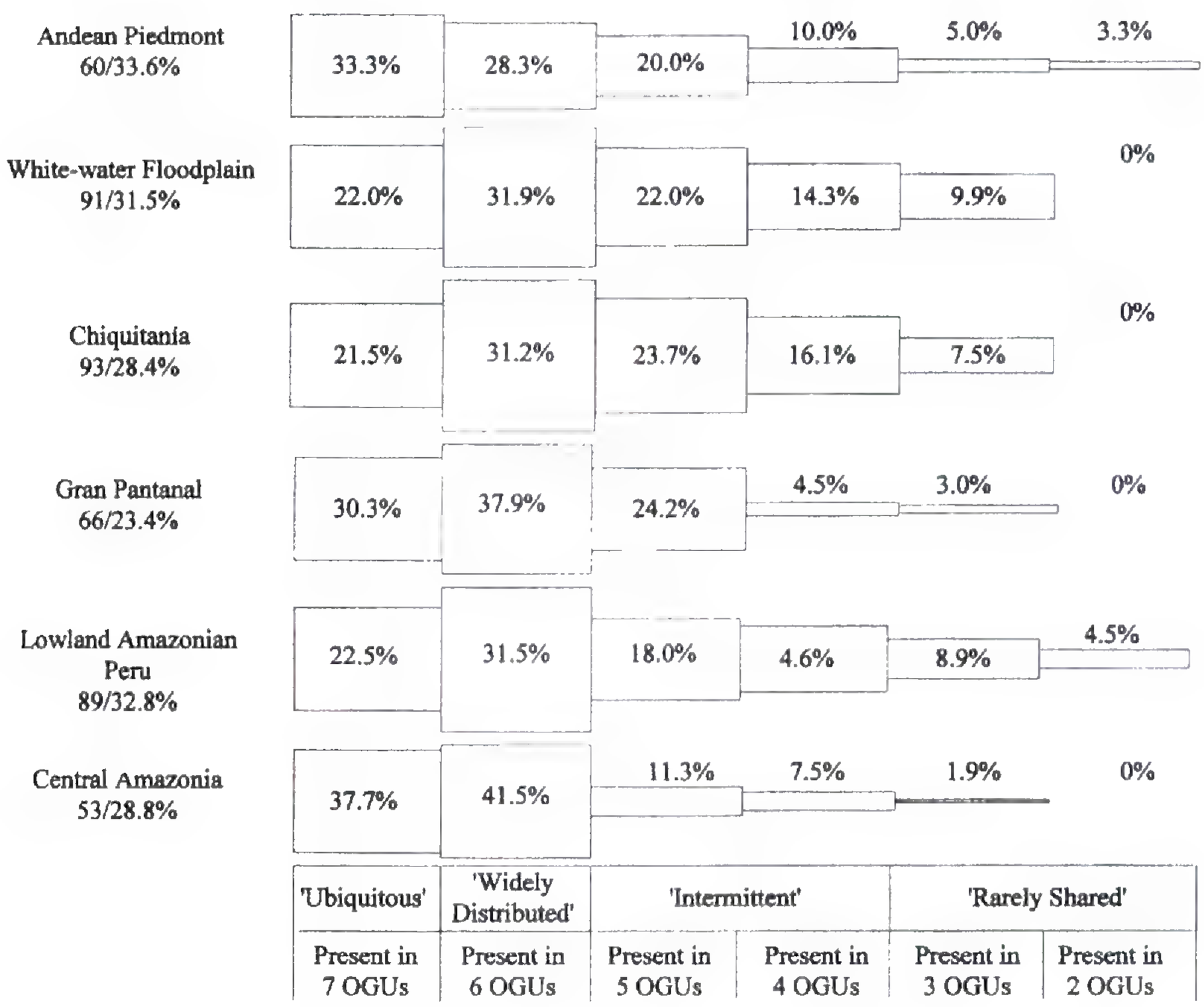

Figure 6. Frequency of species shared between the Chapare and the other Operational Geographic Units (OGUs). Figures below the OGU name indicate the number of species present in both the OGU and the Chapare, followed by floristic similarity (Sørensen's Index). Boxes correspond to species classes (i.e., the number of OGUs in which the species was present) as indicated by the key along the bottom of the figure; the vertical dimension of each box is proportional to the number of species that it represents. Values associated with the boxes indicate the percentage that this portion of the flora contributed to the total species shared between the OGU and the Chapare.

were the Ivirgarsama Marsh, which possessed a well-developed floating mat of *Eleocharis acutangula*, and a few other systems visited during general reconnaissance that possessed poorly developed mats of Poaceae spp. and *Polygonum hydropiperoides*.

Palm swamps, a type of wetland that is common throughout the greatest part of the Bolivian lowlands (e.g., Balslev and Moraes 1989; Beck 1984; Moraes 1991), were not encountered in the Chapare. While it may well be that palm swamps were present in the region, none were observed during this study. Likewise, in the distribution of Bolivian palms presented by Balslev and Moraes (1989) no "wetland palms" [e.g., *Copernicia alba* Morong, *Euterpe precatoria* C. Mart., *Mauritia flexuosa* L. f., *Mauritiella armata* (Mart.) Burret] were listed for the Chapare.

The aquatic herb *Eichhornia azurea* Kunth (Pontederiaceae) is ubiquitous throughout most areas of the Bolivian lowlands, where it frequently contributes to the formation of extensive floating mats of vegetation. Nevertheless, *E. azurea* was not noted in the Chapare. A closely related species, *E. crassipes*, is also commonly encountered in the wetlands of lowland Bolivia and occurs in abundance in some wetlands of the dry Interandean Valleys of the Bolivian Andes (Ritter 2000). Yet, *E. crassipes* was rare in the Chapare. This species was not encountered during fieldwork for this study, nor was it listed for the region by Jiménez (1984); however, Maldonado et al. (1996) did cite a single population.

Submerged macrophytes were not well-represented, with only a few species noted: *Myriophyllum mattogrossense* (Haloragaceae), *Mayaca longipes* (Mayacaceae), and *Eichhornia diversifolia* (Pontederiaceae). The genus *Ludwigia* (Onagraceae) was well-represented (7 species, Appendix). Nevertheless, *L. helminthorrhiza* (Mart.) H. Hara and *L. sedioides* (Humb. & Bonpl.) H. Hara, two aquatic species *sensu stricto* that are very common in other Bolivian lowland regions, were not encountered in the Chapare. The Lentibulariaceae were also poorly represented, with the ubiquitous *Utricularia gibba* the sole species encountered. In contrast, this family was well-represented in the Chiquitanía (17 spp. in two genera), Gran Pantanal (10 spp.), and White-water Floodplain (8 spp.) regions (Ritter 2000).

Despite the Chapare's small wetland flora relative to other Bolivian lowland regions (Table 2), a number of noteworthy species were present. The herb *Tonina fluviatilis* (Eriocaulaceae) covered portions of the Mariposa Wetland. Although the Eriocaulaceae are fairly well-represented in Bolivia's wetlands, with at least 5 genera and 17 species (Ritter 2000), *T. fluviatilis* was the sole member of the family encountered in the Chapare. Although *T. fluviatilis* is widely distributed (Mexico to Central South America, Cuba, and Trinidad; Huft 1994), in Bolivia this species is apparently known only from three widely separated sites: the Mariposa Wetland, a wetland in the Pando (extreme northern Bolivia), and a recently encountered population in eastern Bolivia, in Parque Nacional Noel Kempff Mercado (Ritter 2000). Surprisingly, despite the appreciable fieldwork undertaken by Haase and Beck in the extensive inundated savannas of central Bolivia (Beck 1984; Haase 1989, 1990; Haase and Beck 1989), this species apparently is yet to be collected in that region.

The submersed macrophyte *Apalanthe granatensis* (Hydrocharitaceae) was present in abundance in the Senda F Wetland. Although this species possesses a fairly broad distribution (Colombia to Bolivia), it was previously reported for Bolivia from a single population (Cook 1985).

Nevertheless, *A. granatensis* was observed in a number of roadside pools and marshes in the Chapare, with additional populations noted in the Andean Piedmont region (Ritter 2000).

The wetland shrub *Ludwigia latifolia* (Onagraceae) is also widely distributed, ranging from Nicaragua southwards to Brazil and Bolivia (Ramamoorthy and Zardini 1987). In Bolivia, *L. latifolia* was previously known from a single record: a population in the Chapare along the Río Isarsama. Nevertheless, *L. latifolia* appeared to be fairly common in this region, as during this study additional populations were encountered along three streams.

Other noteworthy species were the rare *Myriophyllum mattogrossense* (Haloragaceae), a submersed macrophyte which had previously not been known for the country (see Crow and Ritter 1999), and the waterlily *Nymphaea glandulifera* (Nymphaeaceae), which was previously known for Bolivia from a single population in the White-water Floodplain (see Ritter et al. 2001). The Chapare appeared to constitute the southern limit for a number of wetland species (e.g., *N. glandulifera*, *Ludwigia latifolia*. *Apalanthe granatensis*, *M. mattogrossense*, and *Tonina fluviatilis*).

Biodiversity. Based solely on number of species, the Chapare study sites could be characterized as species-poor. These systems each possessed only 5–49 species (Table 1), while systems from the other Bolivian lowland OGUs ranged in richness from 25–124 species (Ritter 2000). Nevertheless, there were large-scale differences in the areas of the sites considered in this comparison (i.e., 0.15 ha in the smallest Chapare site to > 30,000 ha in the largest lowland Bolivian site) and larger sites would generally be expected to contain more species (cf. Rosenzweig 1995).

A more accurate comparison of diversity can be seen in the species-area curve of data from the Chapare sites augmented with data from an additional 16 Bolivian lowland wetland systems (Figure 2). The Chapare sites, with four of seven systems located well below the regression line. could generally be considered as species-poor. However, in a larger study of the wetlands of Bolivia (Ritter 2000), the various wetland types (e.g., ponds, marshes, etc.) were found to be characteristically species-rich or -poor. Three of the four Chapare systems located below the regression line were either ponds or lakes, and these wetland types were generally found to be species-poor (Ritter 2000). Thus, the question arises whether or not the characterization of the wetlands of the Chapare as species-poor was due primarily to the regional sample having a fairly large proportion of species-poor wetland types. Still, as the two least diverse Bolivian

lowland marshes (a species-rich wetland type, Ritter 2000) were from the Chapare, it seems likely that the region's wetlands were, indeed, species-poor.

Additional corroboration of the species-poor nature of Chapare wetlands can be seen in the study of 11 lacustrine systems by Maldonado et al. (1996). While the researchers' primary objectives were the characterization of the physicochemical condition of the lakes and the cataloging of the microflora and microfauna, the authors also compiled a checklist of the systems' vascular plant flora. Their study sites were much larger than the sites considered here (with the exception of the Puerto Villarroel Laguna), ranging in area from 7.75–84.25 ha. In total, 29 species were noted; however, because all specimens were not identified, the authors presented only a partial checklist of 19 species. Site-level species-richness from this portion of the vascular flora ranged from 3–12 species; thus, species-richness could potentially have ranged from 13–22 species (i.e., if all ten unidentified species were present at each site). This level of diversity is even lower than what was encountered at the seven Chapare systems considered here and is much lower than that of equivalent-sized systems in other Bolivian lowland areas. For example, the two study sites listed for the Andean Piedmont region by Ritter (2000) were each about 15 ha in area and possessed 71 and 76 species.

At the regional level, the Chapare possessed the fewest species (113; Table 2), and the Chiquitanía the most species (541). However, as with site-level comparisons, a true measure of diversity requires that regional area also be considered. It would be ideal in a study of wetland habitats if regional area were calculated from just the area of inundated habitats within a region. Although I was able to estimate the extent of inundated area for the Bolivian lowland regions, I was unable to confidently do so for all OGUs considered here. Thus, total regional area was substituted as a surrogate for regional wetland area. As demonstrated in Ritter (2000), this approach appears to be sound. It was evident from a plot of the regional species-area data (Figure 3) that the Chapare could, indeed, be considered species-poor, as it was situated well below the regression line. Other species-poor OGUs were Lowland Amazonian Peru and the White-water Floodplain. By contrast, the Andean Piedmont region, which is contiguous with the Chapare, was the richest OGU.

Low species richness in the Chapare wetlands is not in accordance with what is known for terrestrial habitats in the Andean forelands (e.g., Gentry 1988b; Salo et al. 1986). Gentry (1988a) determined that phytodiversity in the Neotropics was strongly correlated with precipitation. The richest forests were found in high rainfall areas

Table 3. Presence of the Alismatidae and the Alismataceae and estimated mean annual precipitation in selected Operational Geographic Units (OGUs). Precipitation data were estimated from the following sources: the Chapare, Morris et al. (1983); the White-water Floodplain, Andean Piedmont, and Chiquitanía Regions, Hanagarth (1993), Killeen et al. (1993), and the Servicio Nacional de Meteorología e Hidrología, La Paz; Central Amazonia, Ratisbona (1976); Lowland Amazonian Peru, Johnson (1976). Note: the Río Paraná Delta region was excluded from these comparisons because it is situated far outside of the limits of Amazonia.

Region (OGU)	Mean Annual Precipitation (mm/yr)	Alismatidae Overall			Alismataceae
		Families	Genera	Species	Species
Gran Pantanal	1100	5	9	23	13
Chiquitanía	1200	5	8	15	10
White-water Floodplain	1650	5	8	15	9
Andean Piedmont	1700	5	9	12	4
Central Amazonia (Brazil)	2000	3	3	3	1
Lowland Amazonian Peru	2600	5	9	18	11
Chapare	3500	3	4	4	1

(3000–4000 mm) with an aseasonal distribution of precipitation (Gentry 1988a, 1992). Gentry (1988a) also noted that under very wet conditions the relationship became linear, with an asymptote reached at annual precipitation levels of around 4000–4500 mm.

Nevertheless, the low diversity of the Chapare wetlands was not entirely unexpected, as a positive correlation between species richness and a pronounced dry season had previously been noted in one group of aquatic plants by Haynes and Holm-Nielsen (1989). The authors noted a scarcity of species in the subclass Alismatidae in Neotropical regions that did not experience a pronounced wet-and-dry seasonality. Assuming that areas with low mean annual precipitation will generally possess a longer dry season than areas with high mean annual precipitation, this correlation can be evidenced among the OGUs considered here (Table 3). Two of the three wettest OGUs (the Chapare and Central Amazonia) were clearly poorest in representatives of the Alismataceae, and of the Alismatidae in general, while the driest OGUs were generally richest. An exception was the third "wet" OGU, Lowland Amazonian Peru, which possessed the second greatest number of species at both the subclass and familial levels. Nevertheless, Lowland Amazonian Peru does include areas with relatively low annual precipitation (Instituto Geográfico

Nacional 1989); hence, it seems reasonable that at least a portion of the species of Alismatidae noted for this region were restricted to these drier areas.

A similar pattern was evident when considering the total wetland floras of the OGUs. It can be seen from the plot of the regional species-area data (Figure 3) that both the wettest (Chapare) and the third-wettest (Lowland Amazonian Peru) OGUs could be considered as species-poor (i.e., situated below the regression line) OGUs. Additionally, a negative correlation between species richness and precipitation can be evidenced in the difference in diversity between the Chapare and the Andean Piedmont. These regions were approximately equal in area (Table 2) and were situated adjacent to each other along the base of the Andes. Yet, the markedly drier Andean Piedmont region (mean annual precipitation = ca. 1700 mm/yr) possessed more than twice as many wetland species (244 spp.; Table 2) as the Chapare (113 spp.). Furthermore, in the comparison with the general trend of diversity in the Neotropical wetland flora (Figure 3) the Andean Piedmont region was shown to be pronouncedly more diverse. I am inclined to think that if species richness and precipitation data were compiled from a series of small, equal-area samples (i.e., 5000 km^2), commencing with the Chapare and proceeding northwards and eastwards out onto the Beni basin, a negative correlation between these two factors would be demonstrated. The current state of both botanical and meteorological data from this region precludes this comparison.

Factors other than precipitation are thought to contribute to the high levels of phytodiversity in Amazonia. The long-held view of Amazonian rainforests has emphasized stability, with forest regeneration seen as occurring predominantly in gaps from treefall (Salo et al. 1986). But, in the last two decades, researchers investigating the effects of floodplain dynamics on lowland Amazonian forests have formulated various hypotheses regarding the contribution of hydrology to forest formation, structure, and diversity (e.g., Kalliola et al. 1991; Puhakka et al. 1992; Salo 1987; Salo et al. 1986). It is now recognized that a significant portion of lowland Amazonian forest is growing upon substrata of fluvial origin. In western Amazonia even forests that are currently unflooded have their origins in the processes that are characteristic along present-day rivers (Kalliola et al. 1991). The lateral erosion and channel migration of the meandering rivers in this region are thought to bring about large-scale natural disturbance and initiate primary succession (Salo et al. 1986). Accretion, erosion, and channel migration serve as a constant form of disturbance in this region, creating a mosaic of forests of different age structure; approximately 0.2% of the area of the active

meander plains and 0.02% of the Peruvian lowlands is eroded annually through these processes (Puhakka et al. 1992).

Salo et al. (1986) proposed that the high levels of disturbance associated with the effects of current and past river dynamics is partially responsible for the elevated biological diversity of the upper Amazon basin. They suggested that: 1) erosion and deposition created a variety of habitats, which, as forest succession and erosion went forward, resulted in a mosaic of different aged forest and soil types; 2) competitive exclusion was precluded because these habitats were fairly short-lived and were highly stable in species composition; and 3) there was a large degree of variation in water and soil chemistry, mode of sedimentation, and "case-historical biogeographical events" (Salo et al. 1986, p. 257). The authors also proposed that, as a result of the high site turnover, intense disturbance, and the resulting varied forest structure, fluvial dynamics might be a major factor in creating and maintaining the high ß-diversity characteristic of the upper Amazon basin. Nevertheless, as Puhakka et al. (1992) have pointed out, the relationship between vegetation patterns and river types are poorly understood; hence, it is difficult to assess the influence that fluvial dynamics may have had on a region's biota.

Although fluvial dynamics may be positively linked with phytodiversity in lowland Amazonian terrestrial habitats, these forces appear to negatively impact the Chapare's wetlands. As river channels shift, oxbow and strand lakes are frequently formed. Many of these persist as lacustrine systems, but others may be reincorporated into the river's mainstem when the sediment dams separating them from the main channel are breached by flooding and erosion. These transitions can occur over a fairly short period of time. For example, during field research a journey was taken up the Río Ichilo to visit a large (ca. 8 km long) oxbow lake that had formed approximately two years previously (based on estimates provided by local fishermen). Upon arrival, it was found that the barriers separating the oxbow from the river had eroded, and the oxbow was once again joined with the Ichilo.

Nevertheless, many of these systems can persist as isolated basins and will undergo various stages of lake-fill (i.e., "successional stages") over time. I examined a number of such systems during this study and all appeared to be species-poor. The flora differed from system to system but, in contrast to what is known for Amazonian terrestrial habitats, it was not evident that there were particular sets of species associated with various successional stages. Furthermore, in Bolivian lowland wetlands it appeared that systems with well-developed floating mats of vegetation generally were the most speciose, in part because of the capability of

these mats to become secondarily colonized by other taxa. As noted, floating mats were generally lacking or poorly developed in Chapare wetlands, and it seems likely that the aforementioned fluvial dynamics have contributed to their scarcity.

In extensive areas of lowland South America, wetlands are subjected to large-scale, regular, seasonal hydrological pulses. Rather than functioning as a disturbance and therefore limiting species richness, some researchers consider that these regular, monomodal pulses enhance diversity (e.g., Junk 1997; Junk et al. 1989; Prado et al. 1994). The rivers of the Chapare, however, do not experience regular seasonal pulses. Instead, they fluctuate in response to precipitation in the upslope regions from which their tributaries flow. Although it may be that the absence of a monomodal hydrologic pulse is associated with the low diversity of the Chapare wetlands, there is still some question as to whether or not these pulses characteristically have a positive effect on phytodiversity (see Ritter 2000).

Any discussion of Chapare ecosystems needs to take into account anthropogenic disturbance. As noted, extensive portions of the Chapare have been converted to the production of coca (*Erythroxylum coca*), with the greatest part intended for the manufacture of cocaine. Enormous quantities of various chemicals (e.g., ammonia, ether, kerosene, potassium permanganate, sodium bicarbonate, and sulfuric acid; Henkel 1995) are used each year in the extraction of coca paste, the first step of cocaine processing. As of the early 1990s, an estimated 4000–5000 coca paste-producing laboratories were operating in the Chapare, with the chemicals used in the extraction process disposed of on site. Although it seems likely that diversity in the Chapare might be negatively impacted by such extensive chemical pollution, there is some evidence that this is not yet the case (Southwest Research Associates Inc. 1993, cited in Henkel 1995). Nevertheless, the region has unquestionably been subjected to extensive anthropogenic modifications in recent decades, and the assumption that these activities must have had some negative impact on diversity in the region's wetlands seems warranted.

Floristic similarities. At the site level, floristic similarities (Sørensen's Index) were generally low, ranging from 0–43%. In contrast, floristic similarities between aquatic systems of the Bolivian portion of the Gran Pantanal de Mato Grosso ranged from 39–58% (Ritter 2000). All of the systems in the Pantanal study (with one exception) were much larger (i.e., 3000–20,000 ha) than the Chapare sites, all but one of which were less than 2 ha. Thus, the Chapare site's low floristic similarities were

undoubtedly partially attributable to sample size. Furthermore, despite their generally low floristic similarities, the majority of the Chapare study sites were situated in close proximity in an ordination (DCA) of the 46 Bolivian study sites (Figure 4). The two systems that were disjunct (in ordination space) from the other Chapare study sites had extremely small floras (5 and 6 species), and their positions in the ordination were most likely due to their possessing one or two species that were common in most lowland systems but absent from the other Chapare sites.

As all but one of the Chapare sites were quite small, it is not clear whether the low floristic similarities were the result of high ß-diversity in the region's wetland flora, or if they were merely an artifact of system size. To elaborate, regions will possess a number of common species (which will serve to elevate calculated floristic similarities), and as the number of species present in small sites will, on average, be less than in large sites, the number of common (and thus, commonly shared) species encountered in small sites will, on average, be less than in large sites.

At the regional scale, the Chapare wetland flora appeared to possess equivalent floristic affinities (as calculated by Sørensen's Index) with the more northern Amazonian OGUs as with the other Bolivian lowland regions. However, the ordination of OGU floras by DCA (Figure 5) indicated that, as might be expected, the Chapare was more closely associated with the lowland Bolivian OGUs than with the extra-Bolivian Amazonian OGUs.

Although the ordination suggested a close floristic association among the lowland Bolivian OGUs, this relationship was not nearly so evident from the histograms of the species frequency classes (Figure 6). The relationships between the Chapare wetland flora and the other OGUs consistently followed the same general pattern, with "ubiquitous" (present in all OGUs) and "widely shared" species (present in six OGUs) contributing the greatest amount to floristic similarities. The largest contribution of "rarely shared" species (restricted to 2–3 OGUs) to floristic similarity was between the Chapare and the spatially disjunct (both geographically and in ordination space; Figure 5) Lowland Amazonian Peru (13.4%). It had been hoped that both the ordination and the frequency analysis would provide evidence that the "wetter" OGUs were closely associated; however, in neither case was a close relationship suggested.

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APPENDIX

SPECIES ASSOCIATED WITH WETLANDS IN THE CHAPARE REGION

Taxa marked with an asterisk (*) are considered to be non-native to Bolivia, as determined from the literature. Abbreviations for study sites are as follows: MW, Mariposa Wetland; IM, Ivirgarsama Marsh; SF, Senda F Wetland; VT, Villa Tunari Pond; SP, Sinahota Pond; PV, Puerto Villarroel Laguna; SC, Valle de Sajta Curichi; GC, General Collecting. Abbreviations for abundance are as follows: A, Abundant; F, Frequent; C, Common; O, Occasional; R, Rare; LA, Locally Abundant; NN, Not Noted. Taxa without listed voucher specimens are those known to be associated with Neotropical wetlands or that were noted in the Chapare by other researchers [data compiled from Jiménez 1984, Maldonado et al. 1993, and w^{3}TROPICOS (Missouri Botanical Garden VAST nomenclatural database. Website: http://mobot.mobot.org/3WT/Search/vast.html)].

POLYPODIOPHYTA (Ferns)

HYMENOPHYLLACEAE. *Trichomanes rigidum* Sw. – Emergent herb; GC/NN.

LYCOPODIACEAE. *Lycopodium clavatum* L. – Trailing herb; MW/O, IM/LA *N. Ritter 3821* (BOLV, LPB, MO, NHA).

MARATTIACEAE. *Danaea elliptica* Sm. – Emergent herb; GC/NN.

PTERIDACEAE. *Ceratopteris pteridoides* (Hook.) Hieron. – Free-floating herb; SC/F, GC/A *N. Ritter 1685* (BOLV, LPB, MO, NHA, W). *Pityrogramma calomelanos* (L.) Link – Emergent herb; IM/O *N. Ritter 3161* (BOLV, NHA).

SALVINIACEAE. *Salvinia minima* Baker – Free-floating herb; SC/F *N. Ritter 1689* (BOLV, LPB, MO, NHA).

THELYPTERIDACEAE. *Thelypteris interrupta* (Willd.) K. Iwats. – Emergent herb; IM/C *N. Ritter 2980* (BOLV, LPB, MO, NHA, W). *Thelypteris serrata* (Cav.) Alston – Emergent herb; MW/C, IM/C, VT/R *N. Ritter 3156* (BOLV, NHA). *Thelypteris* sp. – Emergent herb; IM/LA *N. Ritter 3820* (BOLV, LPB, MO, NHA, W).

MAGNOLIOPHYTA (Angiosperms)

MAGNOLIOPSIDA (Dicotyledons)

ACANTHACEAE. *Hygrophila costata* Nees – Emergent herb; GC/LA *N. Ritter 3148* (BOLV, LPB, MO, NHA, USZ). *Justicia comata* (L.) Sw. – Emergent herb; VT/A, GC/LA *N. Ritter 1613* (BOLV, LPB, MO, NHA, W).

ANACARDIACEAE. *Tapirira guianensis* Aubl. – Tree; GC/NN.

APOCYNACEAE. *Mandevilla hirsuta* (Rich.) K. Schum. – Climber; MW/O *N. Ritter 3849* (BOLV, LPB, MO, NHA). *Odontadenia geminata* (Hoffmanns. *ex* Roem. & Schult.) Müll.Arg. – Climber; MW/R *N. Ritter & M. Ritter 3853* (BOLV, NHA). *Prestonia acutifolia* (Benth. *ex* Müll.Arg.) K. Schum. Climber; SF/O *N. Ritter 1620* (BOLV, LPB, MO, NHA). *Rhabdadenia macrostoma* (Benth.) Müll.Arg. – Climber; SC/O *N. Ritter 1688* (BOLV, LPB, MO, NHA).

ASCLEPIADACEAE. *Cynanchum montevidense* Spreng. - Climber; GC/O *N. Ritter & M. Ritter 3855* (BOLV, MO, NHA). *Tassadia graziela*e Fontella – Climber; MW/A, IM/LA *N. Ritter 1439* (BOLV, LPB, MO, NHA, W).

ASTERACEAE. *Barroso*a *confluentis* (B. L. Rob.) R. M. King & H. Rob. – Emergent herb; IM/R *N. Ritter 2985* (BOLV, LPB, MO, NHA, W). *Eclipta prostrata* (L.) L. – Emergent herb; SP/R *N. Ritter 1439* (BOLV, MO, NHA). **Erechtites hieraciifolia* Raf. *ex* DC. – Emergent herb; IM/O *N. Ritter 3833* (BOLV, NHA). *Mikania congesta* DC. - Climber; SF/C *N. Ritter 3141* (BOLV, MO, NHA). *Mikania psilostachya* DC. – Climber; MW/F *N. Ritter 1641* (BOLV, LPB, MO, NHA, W). *Tessaria integrifolia* Ruiz & Pav. – Tree; GC/A.

BEGONIACEAE. *Begonia fischeri* Schrank Emergent herb; IM/O *N. Ritter 2981* (BOLV, NHA, USZ).

BORAGINACEAE. *Cordia tetrandra* Aubl. - Tree; GC/NN.

CABOMBACEAE. *Cabomba furcata* Schult. & Schult. f. - Submersed herb; GC/A *N. Ritter 3812* (BOLV, LPB, MO, NHA).

CAMPANULACEAE. *Centropogon cornutus* (L.) Druce – Emergent herb; MW/LA, IM/C *N. Ritter & G.E. Crow 2310* (BOLV, LPB, MO, NHA, W).

CHRYSOBALANACEAE. *Hirtella triandra* Sw. – Tree; GC/NN.

CLUSIACEAE. *Calophyllum brasiliense* Cambess. – Tree; GC/NN. *Vismia* sp. – Tree; IM/R *N. Ritter 3818* (BOLV, NHA).

CONVOLVULACEAE. *Ipomoea* cf. *phillomega* House – Climber; IM/O *N. Ritter 3163* (BOLV, LPB, NHA).

DILLENIACEAE. *Davilla nitida* (Vahl) Kubitzki – Climber; IM/R *N. Ritter 3816* (BOLV, MO, NHA).

ERYTHROXYLACEAE. *Erythroxylum coca* Lam. – Shrub; IM/R *N. Ritter 3819* (BOLV, MO, NHA).

EUPHORBIACEAE. *Caperonia palustris* (L.) A. St.-Hil. – Emergent herb, at times free-floating; SF/O, GC/C *N. Ritter 1399* (BOLV, LPB, MO, NHA, W).

FABACEAE. *Aeschynomene rudis* Benth. – Emergent herb; GC/A *N. Ritter & G.E. Crow 2315* (BOLV, LPB, MO, NHA, W). *Desmodium adscendens* (Sw.) DC. – Climber; MW/C, IM/C *N. Ritter 3825* (BOLV, NHA). *Inga umbellifera* (Vahl) Steud. *ex* DC. – Tree; GC/NN. *Mimosa pigra* L. – Shrub; GC/F *N. Ritter 1399* (BOLV, LPB, MO, NHA). *Phaseolus* sp. – Climber; MW/R, IM/C *N. Ritter 3825* (BOLV, NHA). *Zygia cauliflora* (Willd.) Killip *ex* Record – Tree; SF/O *N. Ritter & G.E. Crow 1121* (BOLV, MO, NHA). Indet. – Emergent herb; MW/C *N. Ritter 3846* (BOLV, NHA).

HALORAGACEAE. *Myriophyllum mattogrossense* Hoehne – Submersed herb; GC/LA *N. Ritter 3147* (BOLV, GH, LPB, MO, NHA, USZ).

LAMIACEAE. *Hyptis atrorubens* Poit. Emergent herb; MW/LA *N. Ritter 1636* (BOLV, LPB, MO, NHA, W). *Hyptis brevipes* Benth. – Emergent herb; SP/O *N. Ritter 1395* (BOLV, LPB, MO, NHA). *Hyptis lacustris* A. St.-Hil. *ex* Benth. – Emergent herb; IM/O *N. Ritter 3157* (BOLV, LPB, MO, NHA).

LENTIBULARIACEAE. *Utricularia gibba* L. – Suspended aquatic herb; IM/O *N. Ritter 3836* (BOLV, NHA).

LORANTHACEAE. *Phthirusa pyrifolia* (Kunth) Eichler – Parasite; MW/C, IM/O *N. Ritter 3847* (BOLV, LPB, MO, NHA).

LYTHRACEAE. *Cuphea melvilla* Lindl. – Shrub; PV/F *N. Ritter 1680* (BOLV, LPB, MO, NHA, W).

MALVACEAE. *Hibiscus sororius* L. Emergent herb; PV/O *N. Ritter 1682* (BOLV, LPB, MO, NHA, W). *Pavonia fruticosa* (P. Mill.) Fawc. & Rendle – Emergent herb; VT/O *N. Ritter 1646* (BOLV, LPB, MO, NHA, W).

MELASTOMATACEAE. *Aciotis acuminifolia* (Mart. *ex* DC.) Triana – Emergent herb; MW/O, IM/LA, GC/LA *N. Ritter 1637* (BOLV, LPB, MO, NHA, W). *Aciotis caulialata* (Ruiz & Pav.) Triana Emergent herb; MW/O *N. Ritter 3842* (BOLV, MO, NHA). *Clidemia* cf. *biserrata* DC. – Shrub; MW/C *N. Ritter 1640* (BOLV, LPB, MO, NHA, W). *Clidemia capitellata* (Bonpl.) D. Don Shrub; IM/NN *N. Ritter 3158* (BOLV, MO, NHA, US). *Miconia ampla* Triana Shrub; MW/A, IM/R *N. Ritter & G.E. Crow 2294* (BOLV, LPB, MO, NHA, W). *Miconia tomentosa* (Rich.) D. Don – Shrub; IM/R *N. Ritter 3815* (BOLV, LPB, MO, NHA, US). *Miconia* sp. Shrub; MW/O *N. Ritter 3840* (BOLV, LPB, MO, NHA, US). *Tococa* aff. *macrophysca* Spruce *ex* Triana – Shrub; MW/LA *N. Ritter & G.E. Crow 2295* (BOLV, GH, LPB, MO, NHA, US, W).

MYRTACEAE. *Eugenia florida* DC. – Understory tree; GC/NN. **Psidium guajava* L. – Understory tree; VT/O *N. Ritter 1400* (BOLV, LPB, MO, NHA, W).

NYMPHAEACEAE. *Nymphaea amazonum* Mart. & Zucc. subsp. *amazonum* – Rooted macrophyte with floating leaves; GC/C *N. Ritter & G.E. Crow 2316* (BOLV, LPB, MO, NHA, W). *Nymphaea glandulifera* Rodsch. – Rooted macrophyte with floating leaves; MW/LA *N. Ritter 1642* (BOLV, MO, NHA).

OCHNACEAE. *Sauvagesia erecta* L. – Emergent herb; MW/C, IM/C *N. Ritter 1633* (BOLV, LPB, MO, NHA, W).

ONAGRACEAE. *Ludwigia affinis* (DC.) Hara – Emergent herb; GC/R *N. Ritter 3137* (BOLV, NHA). *Ludwigia decurrens* Walter – Emergent herb; IM/O, GC/LA *N. Ritter & G.E. Crow 3839* (BOLV, GH, LPB, MO, NHA, W). *Ludwigia inclinata* (L. f.) M. Gómez – Emergent herb; SF/C, GC/A *N. Ritter 1614* (BOLV, LPB, MO, NHA, W). *Ludwigia latifolia* (Benth.) Hara – Shrub; GC/O *N. Ritter 2987* (BOLV, LPB, MO, NHA, W). *Ludwigia leptocarpa* (Nutt.) Hara – Emergent herb; SC/O, PV/O, GC/C *N. Ritter 2977* (BOLV, LPB, MO, NHA, W). *Ludwigia nervosa* (Poir.) Hara – Shrub; MW/A, IM/A, SF/C *N. Ritter & G.E. Crow 1112* (BOLV, LPB, MO, NHA). *Ludwigia octovalvis* (Jacq.) Raven – Emergent herb; SF/C, SP/C *N. Ritter 1392* (BOLV, LPB, MO, NHA, W).

PIPERACEAE. *Piper pilirameum* C. DC. – Shrub; MW/C, IM/O *N. Ritter 1639* (BOLV, LPB, MO, NHA, W).

POLYGONACEAE. *Polygonum ferrugineum* Wedd. – Emergent herb; GC/LA *N. Ritter & G.E. Crow 1133* (BOLV, LPB, MO, NHA). *Polygonum hydropiperoides* Michx. – Emergent herb; MW/C, IM/O, SP/F, GC/A *N. Ritter 1391* (BOLV, LPB, MO, NHA, W). *Polygonum meisnerianum* Cham. & Schltdl. – Emergent herb; GC/LA *N. Ritter 1615* (BOLV, LPB, MO, NHA, W). *Polygonum punctatum* Elliott – Emergent herb; SC/A, PV/F *N. Ritter 1687* (BOLV, LPB, MO, NHA, W). *Triplaris americana* L. – Tree; GC/NN.

RUBIACEAE. *Borreria ocymifolia* (Willd. *ex* Roem. & Schult.) Bacigalupo & E. L. Cabral – Emergent herb; GC/LA *N. Ritter 1702* (BOLV, LPB, MO, NHA, W). *Coccocypselum hirsutum* Bartl. *ex* DC. – Emergent herb; MW/LA *N. Ritter & G.E. Crow 2300* (BOLV, LPB, MO, NHA). *Genipa americana* L. – Tree; GC/NN. **Oldenlandia lancifolia* (Schumach.) DC. – Emergent herb; MW/O, IM/O, SF/C, VT/C, SP/F, GC/F *N. Ritter 1701* (BOLV, LPB, MO, NHA, W). *Palicourea riparia* Benth. – Shrub; SF/O *N. Ritter & G.E. Crow 1118* (BOLV, MO, NHA). *Palicourea triphylla* DC. – Shrub; IM/R *N. Ritter 3823* (BOLV, LPB, MO, NHA, USZ, W). *Psychotria poeppigiana* Müll.Arg. – Shrub; MW/F *N. Ritter & G.E. Crow* 2309 (BOLV, GH, MO, NHA, W). *Sabicea novo-granatensis* K. Schum. – Climber; MW/A, IM/O, SF/C, GC/O *N. Ritter 1438* (BOLV, LPB, MO, NHA, W). *Sabicea villosa* Willd. *ex* Roem. & Schult. – Climber; GC/NN. *Spermacoce tenuior* L. – Emergent herb; VT/LA *N. Ritter 1407* (BOLV, LPB, MO, NHA, W).

SAPINDACEAE. *Paullinia pinnata* L. – Climber; SF/O *N. Ritter & G.E. Crow 1120* (BOLV, LPB, NHA).

SCROPHULARIACEAE. *Lindernia* sp. – Emergent herb; SP/LA *N. Ritter 1387* (BOLV, LPB, MO, NHA, W). *Scoparia dulcis* L. – Emergent herb; GC/NN. **Torenia thouarsii* (Cham. & Schltdl.) O. Kuntze – Emergent herb; MW/O, IM/R, GC/C *N. Ritter 1700* (BOLV, LPB, MO, NHA).

SPHENOCLEACEAE. *Sphenoclea zeylanica* Gaertn. – Emergent herb; GC/R.

VITACEAE. *Cissus erosa* Rich. – Climber; GC/LA *N. Ritter 1694* (BOLV, LPB, MO, NHA, W).

LILIOPSIDA (Monocotyledons)

ALISMATACEAE. *Echinodorus* cf. *subalatus* (Mart.) Griseb. – Emergent herb; SF/O *N. Ritter 1617* (BOLV, LPB, MO, NHA, UNA).

ARACEAE. *Pistia stratiotes* L. – Free-floating herb; GC/NN.

COMMELINACEAE. *Commelina* sp. – Emergent herb; MW/NN *N. Ritter 1442* (BOLV, MO, NHA).

COSTACEAE. *Costus arabicus* L. – Emergent herb; IM/F *N. Ritter 3152* (BOLV, MO, NHA). *Costus scaber* Ruiz & Pav. – Emergent herb; GC/NN.

CYPERACEAE. *Calyptrocarya glomerulata* (Brongn.) Urb. – Emergent herb; MW/LA *N. Ritter & G.E. Crow 2305* (BOLV, MO, NHA, W). *Cyperus aggregatus* (Willd.) Endl. – Emergent herb; GC/LA *N. Ritter 3810* (BOLV, LPB, MO, NHA, W). *Cyperus haspan* L. – Emergent herb; MW/F, IM/R *N. Ritter 1635* (BOLV, MO, NHA, W). *Cyperus luzulae* Hochst. *ex* Steud. Emergent herb; IM/O, SF/C, VT/C *N. Ritter 3834* (BOLV, MO, NHA). *Cyperus meyenianus* Kunth – Emergent herb; MW/R, IM/C, SF/O *N. Ritter 3814* (BOLV, LPB, MO, NHA, W). *Cyperus surinamensis* Rottb. – Emergent herb; SP/F *N. Ritter 1394* (BOLV, MO, NHA). *Diplacrum longifolium* (Griseb.) C. B. Clarke – Emergent herb; MW/F *N. Ritter 1630* (BOLV, MO, NHA, W). *Diplasia karataefolia* Rich. – Emergent herb; MW/R *N. Ritter & G.E. Crow 2307* (BOLV, MO, NHA, W). *Eleocharis acutangula* (Roxb.) Schult. – Floating mat-forming herb; IM/A *N. Ritter 2979* (BOLV, LPB, MO, NHA, W). *Eleocharis elegans* (Kunth) Roem. & Schult. – Emergent herb; GC/O *N. Ritter 3135* (BOLV, MO, NHA). *Eleocharis interstincta* R. Br. – Emergent herb; MW/A *N. Ritter 1433* (BOLV, MO, NHA). *Fimbristylis dichotoma* (L.) Vahl – Emergent herb; IM/LA, GC/C *N. Ritter 1704* (BOLV, MO, NHA, W). *Fimbristylis littoralis* Gaudich. – Emergent herb; GC/F *N. Ritter 2978* (BOLV, LPB, MO, NHA, W). *Oxycaryum cubense* (Poepp. & Kunth) Lye – Floating mat-forming herb; IM/O *N. Ritter 3165* (BOLV, NHA). *Scleria cyperinoides* Clark – Emergent herb; MW/C *N. Ritter & G.E. Crow 2299* (BOLV, MO, NHA). *Scleria macrophylla* J. Presl & C. Presl Emergent herb; MW/LA, SF/C, GC/C *N. Ritter 3150* (BOLV, LPB, MO, NHA). *Scleria microcarpa* Nees *ex* Kunth – Emergent herb; SF/O, VT/A *N. Ritter 1402* (BOLV, MO, NHA, W).

ERIOCAULACEAE. *Tonina fluviatilis* Aubl. – Emergent herb; MW/A *N. Ritter 1443* (BOLV, LPB, MO, NHA).

HELICONIACEAE. *Heliconia marginata* (Griggs) Pittier – Emergent herb; SC/A *N. Ritter 1686* (BOLV, LPB, MO, NHA).

HYDROCHARITACEAE. *Apalanthe granatensis* (Humb. & Bonpl.) Planch. – Submersed herb; SF/A *N. Ritter 1621* (BOLV, LPB, MO, NHA, W). *Limnobium laevigatum* (Humb. & Bonpl. *ex* Willd.) Heine – Free-floating herb; GC/NN.

LIMNOCHARITACEAE. *Limnocharis flava* (L.) Buchenau – Emergent herb; GC/R *N. Ritter 1616* (BOLV, LPB, MO, NHA, W).

ORCHIDACEAE. *Campylocentrum minutum* C. Schweinf. – Epiphytic herb; IM/O *N. Ritter 3838* (LPB, MO, NHA, USZ). *Epidendrum schomburgkii* Lindl. – Epiphytic herb; MW/R *N. Ritter & G.E. Crow* (BOLV, MO, NHA). *Trizeuxis falcata* Lindl. – Epiphytic herb; IM/C *N. Ritter 3837* (BOLV, LPB, MO, NHA, USZ, W).

POACEAE. *Acroceras zizanioides* (Humb., Bonpl. & Kunth) Dandy – Emergent herb; GC/A *N. Ritter 2975* (BOLV, NHA, W). *Andropogon bicornis* (L.) Forsk. – Emergent herb; MW/O, IM/O *N. Ritter 3875* (BOLV, NHA). *Andropogon selloanus* (Hack.) Hack. – Emergent herb; MW/O *N. Ritter 1634* (BOLV, LPB, MO, NHA). *Axonopus fissifolius* (Raddi) Kuhlm. – Emergent herb; SP/R *N. Ritter 1393* (BOLV, LPB, MO, NHA). *Coix lacryma-jobi* L. – Emergent herb; GC/LA. *Echinochloa colona* (L.) Link – Emergent herb; GC/O *N. Ritter 2993* (BOLV, LPB, MO, NHA, W). *Gynerium sagittatum* (Aubl.) P. Beauv. – Emergent herb; GC/A. **Hemarthria altissima* (Poir.) Stapf & C. E. Hubb – Emergent herb; GC/LA *N. Ritter, J. Wood, D. Brummitt & D. Wasshausen 3265* (BOLV, LPB, MO, NHA). *Homolepis aturensis* (Humb., Bonpl. & Kunth) Chase – Emergent herb; MW/C *N. Ritter 1629* (BOLV, LPB, MO, NHA). *Hymenachne amplexicaulis* (Rudge) Nees – Emergent herb; GC/A *N. Ritter 1691* (BOLV, LPB, MO, NHA). *Hymenachne donacifolia* (Raddi) Chase – Emergent herb; SF/F *N. Ritter 3139* (BOLV, NHA). **Hyparrhenia rufa* (Nees) Stapf. – Emergent herb; IM/F *N. Ritter 31* (BOLV, LPB, MO, NHA). *Luziola bahiensis* (Steud.) Hitchc. – Emergent herb; MW/O *N. Ritter 1631* (BOLV, LPB, MO, NHA). *Panicum dichotomiflorum* Michx. – Emergent herb; SP/F *N. Ritter 1396* (BOLV, LPB, MO, NHA). *Panicum grande* Hitchc. & Chase – Emergent herb; MW/C *N. Ritter & G.E. Crow 2308* (BOLV, MO, NHA). *Panicum hylaeicum* Mez – Emergent herb; MW/LA *N. Ritter 3843* (BOLV, MO, NHA, US). *Panicum laxum* Sw. – Emergent herb; VT/C *N. Ritter 1403* (BOLV, LPB, MO, NHA). *Panicum mertensii* Roth – Emergent herb; PV/C *N. Ritter 1679* (BOLV, LPB, MO, NHA). *Panicum pilosum* Sw. – Emergent herb; MW/O, VT/C, GC/LA *N. Ritter 2986* (BOLV, LPB, MO, NHA, W). *Panicum polygonatum* Schrad. – Emergent herb; MW/A, IM/LA *N. Ritter 3830* (BOLV, LPB, MO, NHA, W). *Panicum schwackeanum* Mez – Emergent herb; MW/F *N. Ritter 1434* (BOLV, LPB, MO, NHA). *Panicum stoloniferum* Poir. – Emergent herb; VT/C *N. Ritter 1406* (BOLV, LPB, MO, NHA). *Paspalum conjugatum* P. J. Bergius – Emergent herb; GC/NN. *Paspalum repens* P. J. Bergius – Emergent herb; GC/NN. *Steinchisma hians* (Elliott) Nash *ex* Small – Emergent herb; MW/C *N. Ritter 3142* (BOLV, NHA).

PONTEDERIACEAE. *Eichhornia crassipes* (Mart.) Solms – Herb with floating stems and/or petioles (at times free-floating); GC/NN. *Eichhornia diversifolia* (Vahl) Urb. – Herb with floating stems and/or petioles; GC/R *N. Ritter 2974* (BOLV, GH, NHA). *Pontederia rotundifolia* L. f. – Herb with floating stems and/or petioles; SF/A *N. Ritter 1622* (BOLV, LPB, MO, NHA).

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NEIDIUM RUDIMENTARUM (BACILLARIOPHYCEAE), A RARE SPECIES WITH NOVEL RUDIMENTARY CANALS AND AREOLAR OPENINGS FROM THE TEMPERATE REGION OF NORTH AMERICA

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ABSTRACT. *Neidium rudimentarum* is a rare species identified from only two localities in the United States. Rudimentary canals on either side of the valve, that extend 10–25 μm from the terminal apices, are unique to this species within the genus. At the internal termination point, the canals open into chambered areolae that form a well-developed matrix of interconnected chambers. In addition to the canals, linear slits are unique for the external opening of the areolae. The type locality Bluehole pool/Inskip River, New Jersey is a cool water, oligotrophic system with a groundwater source from the Potomac-Raritan-Magothy aquifer. *Neidium hamatum*, from Rio Tapajós, Brazil is the closest known taxon in general morphology, however it has complete longitudinal canals extending from apex to apex. The rudimentary canal of this species is in distinct contrast to the multiple canals of *N. tumescens* and is thus far unique within the genus *Neidium sensu lato*.

Key Words: diatom, North America, rare species, rudimentary canal

In 1959, an interesting *Neidium* species, *Neidium rudimentarum*, was described with longitudinal bands (canals) present only at the apices (Reimer 1959). This incomplete or rudimentary canal formation is unique to this species, especially considering that the primary character for *Neidium* is the presence of longitudinal canals extending along the valve margin. The observed occurrence from two localities in the United States [New Jersey, Winslow, Blue Hole, Inskip River (Boyer Collection, *W-6-23*, ANSP) and New Hampshire, Grafton County, Crane

Pond (*G.C. 53811b*, ANSP)] is also of interest, given the extensive collecting of diatoms across North America from both living and historical sediments. This study examines the morphological structure of *N. rudimentarum* and compares it to related taxa within the genus. Further, the diversity of canal structures is explored with reference to the morphology of the genus *Neidium sensu lato*.

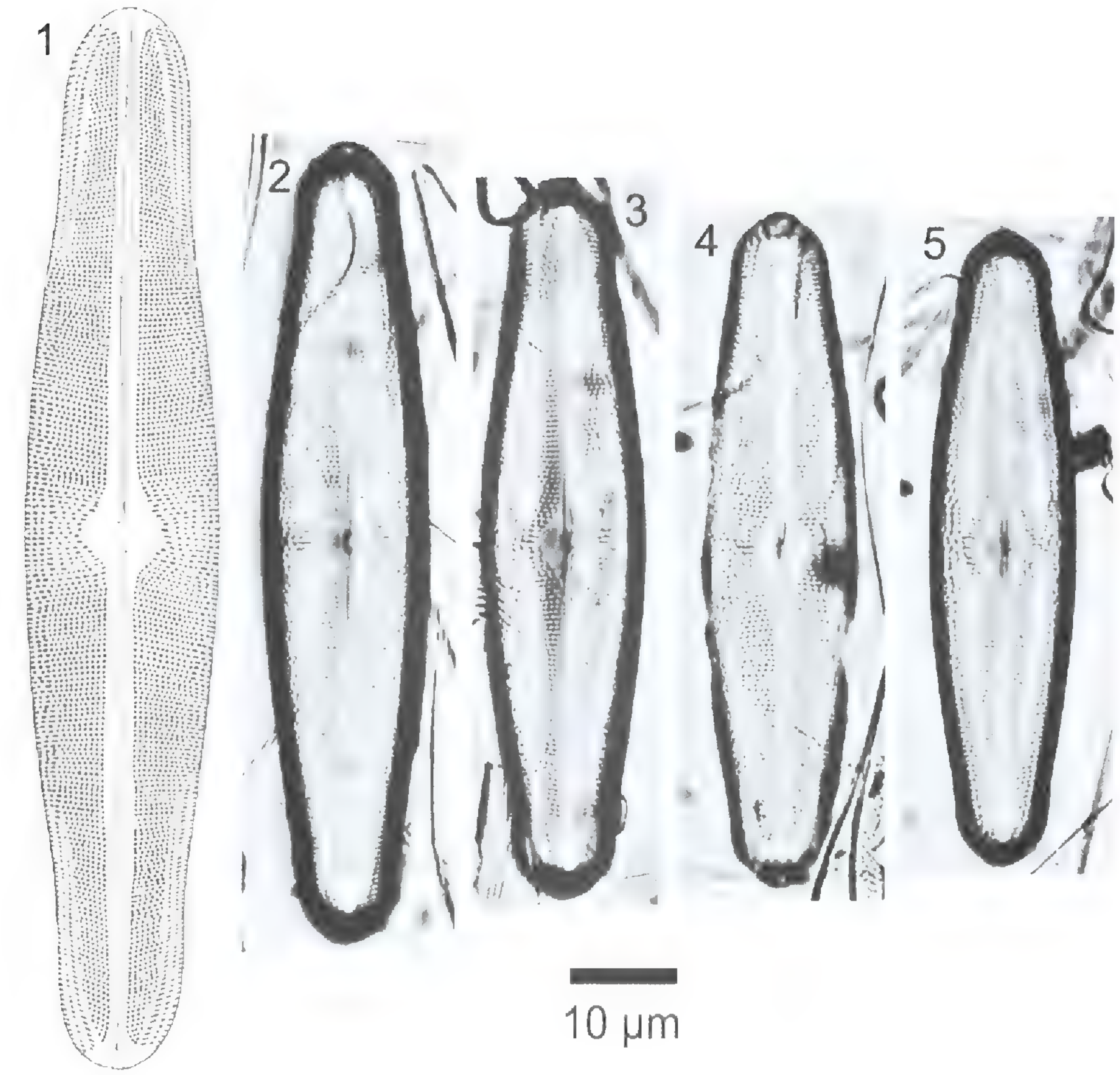
MATERIALS AND METHODS

Specimens of *Neidium rudimentarum* from the holotype slide (*BOYER-W-6-23*, ANSP) were observed and measured using a Wild M20™ microscope equipped with bright field optics. In addition, type material was acquired for examination from the Academy of Natural Sciences (ANSP). The type material was mounted using Hyrax® and deposited at the Canadian Museum of Nature under *68356* (CANA). Morphometric observations were made on the *68356* CANA slide with a Leitz™ Dialux 22 microscope (LM) equipped with bright field and phase contrast optics. Subsamples from the type material were also mounted for scanning electron microscope (SEM) examination following the procedures of Hamilton et al. (1990). An Hitachi S-530 SEM and a FEI XL30 Environmental SEM were used to study detailed morphometric structure using acceleration voltages ranging from 5–15 kV. Diatom terminology follows that of Anonymous (1975), Ross et al. (1979), and von Stosch (1975).

RESULTS

Neidium rudimentarum Reimer, *emend.* Proc. Acad. Nat. Sci. Philadelphia 111: 1–35. 1959. TYPE: U.S.A. New Jersey: Winslow, Blue Hole, Inskip River, 26 May 1923, *T.C. Palmer* (HOLOTYPE: Boyer Collection, *BOYER-W-6-23*, ANSP; subsamples of type material: *68356*, CANA).

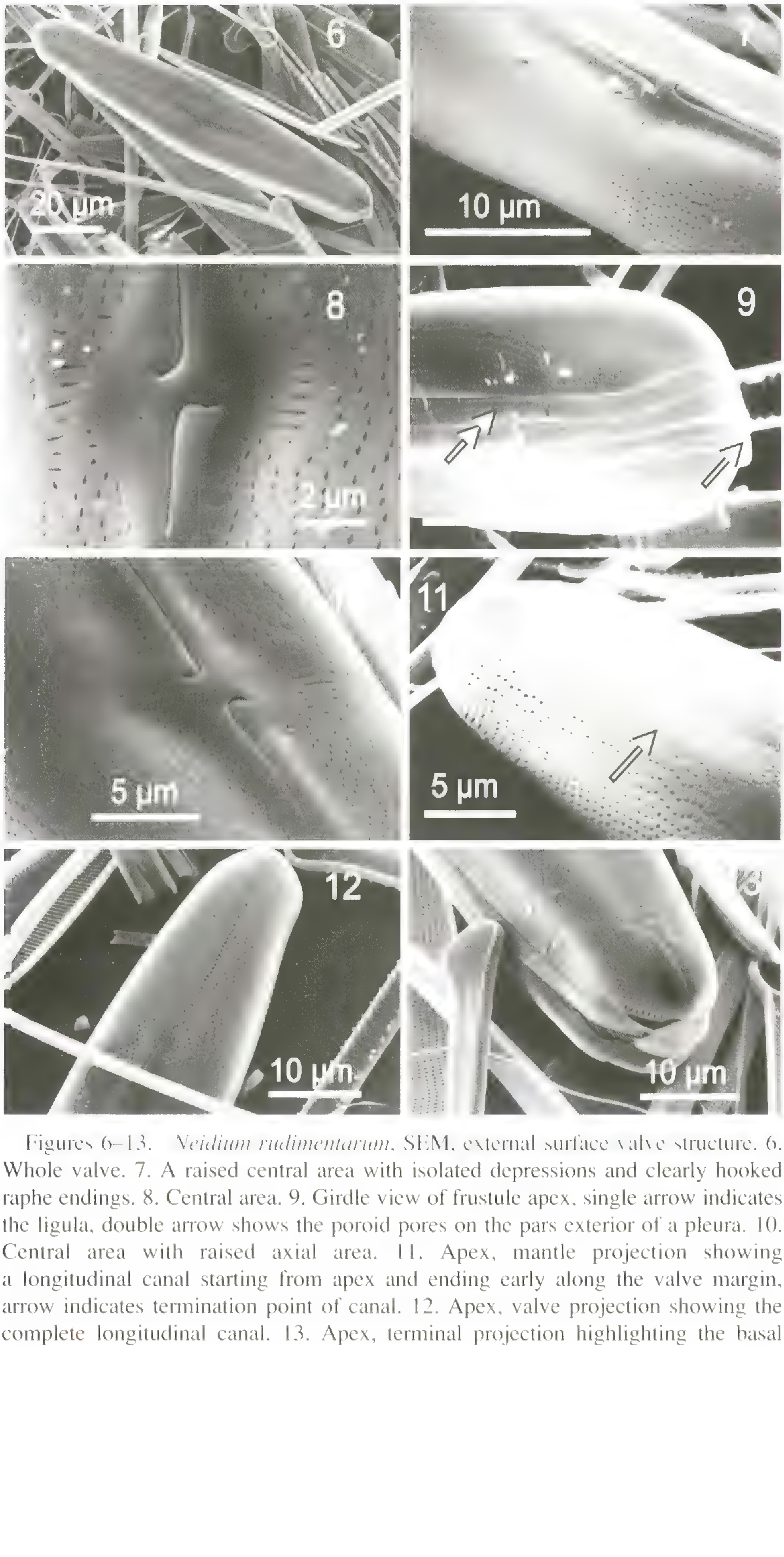
Valves linear to linear-elliptical, 52–110 μm in length, 11–20 μm in width, striae 19–24 in 10 μm with 12–18 areolae in 10 μm (Figures 1–5). Apices are obtusely rounded to subcuneate. The raphe is filiform with deflected central raphe ends that do not terminate in distinct fissures (Figures 1, 3, 5). The terminal raphe fissures are partially covered with an apical flap (lacinia), which appears in LM as a "bifurcation" of the terminal raphe end (Figure 1). The central area is round to slightly elliptical, covering 27–40% of the valve width. Striae around the central area exist as slits that extend towards the valve mantle. The uneven



Figures 1–5. Line drawing and LM photomicrographs of *Neidium rudimentarum*. 1. Line drawing of the holotype printed with permission from Reimer in Patrick & Reimer (1966). 2–5. Bright Field light micrographs taken from *68356*, CANA (two slides).

spacing of areolae, especially evident along the valve margin, creates a "wavy" orientation of these pores, especially around the central area (Figures 1–5). Two longitudinal canals originate from the apices and quickly terminate 10–25 µm from the apex (Figures 1–4). Striae are slightly radiate at the center to slightly convergent at the apices. This emended species description differs from the original (Reimer 1959) by expanding the size range, increasing the stria count, introducing an areola count, and clarifying the ultrastructure of the longitudinal canal and areolae.

Externally, the valve shows many structural characters that differ from other *Neidium* species (Figures 6–13). The raphe is composed of two straight branches running the length of the valve and sits on a solid



Figures 6–13. *Veidium rudimentarium*, SEM, external surface valve structure. 6. Whole valve. 7. A raised central area with isolated depressions and clearly hooked raphe endings. 8. Central area. 9. Girdle view of frustule apex, single arrow indicates the ligula, double arrow shows the poroid pores on the pars exterior of a pleura. 10. Central area with raised axial area. 11. Apex, mantle projection showing a longitudinal canal starting from apex and ending early along the valve margin, arrow indicates termination point of canal. 12. Apex, valve projection showing the complete longitudinal canal. 13. Apex, terminal projection highlighting the basal

(non-ornamented) axial area, which is elevated at the terminal apices (Figures 6, 9, 11, 12). The axial area at the center of the valve is also elevated and surrounded by a depressed central area (Figures 7, 8, 10). The raphe terminates at the mantle under a small but distinct lacinia that extends to the mantle base (Figures 9, 13). Striae are composed of linear slit-like areolae, which become slightly rounded to elliptical along the mantle face (Figures 7, 8, 10, 11). Long elliptical areolae also exist along the base of the mantle at the apices (Figure 13). Around the central area, the first set of areolae are lineolate and oriented perpendicular to other areolae creating the slits observed in LM (Figures 8, 10). The central area is clearly elevated and may sometimes have depressions, which are not areolae (Figure 8). When the valve deteriorates, the areolae may become round in appearance (Figure 11). The longitudinal canal does not extend far from the apices and terminates into two or more areolae (Figures 6, 11, 12). Three to four pleurae are typically present with a complete frustule. The pleurae are incomplete ligulate bands opening alternately at the apices (Figures 9, 13). Each pleura has one row of pores along the upper pars exterior edge.

Internally, the raphe is elevated on the sternum, ending terminally in helictoglossae and centrally with a bimodal central nodule (Figures 14, 15, 16). The raphe is a key and slot formation. The small longitudinal canals at the apices open internally through enlarged elliptical slits that are especially evident at the apex (Figures 15, 17). The equally spaced areolae are round to elliptical with beveled edges, creating a poroid internal surface. The areolae are composed of small internal chambers within the siliceous valve structure and connect to other adjacent areolae and the longitudinal canal (Figures 14, 16, 18, 19). Other taxa with this type of open-chambered or interconnected areolae include *Neidium amphigomphus* (Ehrenb.) Pfitzer., *N. ampliatum* (Ehrenb.) Krammer, *N. gracile* Hust., *N. hitchcockii* (Ehrenb.) Cleve, and *N. tumescens* (Grunow) Cleve (Hamilton et al. 1995; Reichardt 1995; Siver et al. 2003; unpubl. images). No hymen structures were found on the few specimens observed, however it is presumed that hymens would be present and cover the internal openings of the areolae. This assumption is based on the consistent presence of hymens in other *Neidium* taxa with a similar areolate structure.

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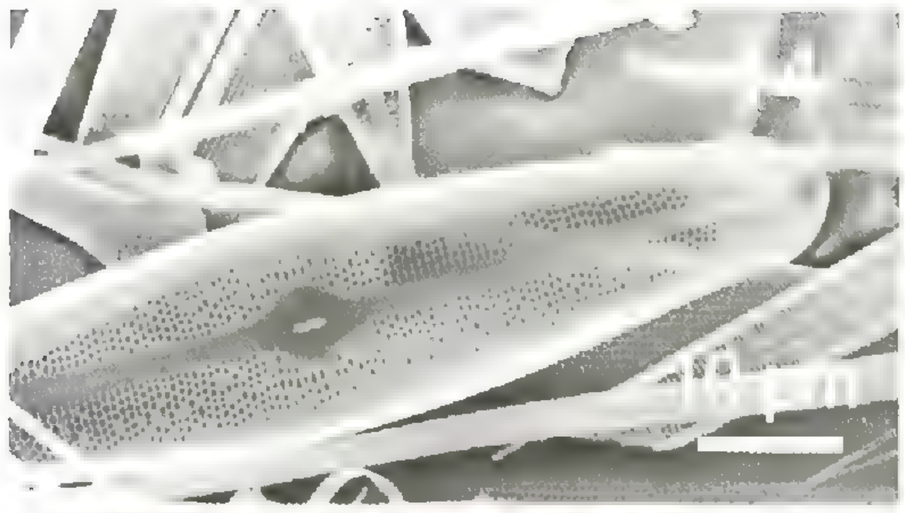
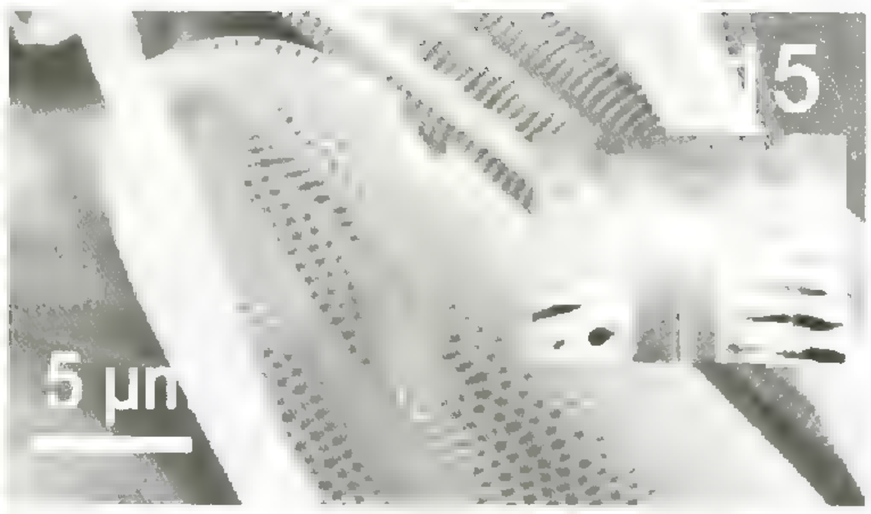
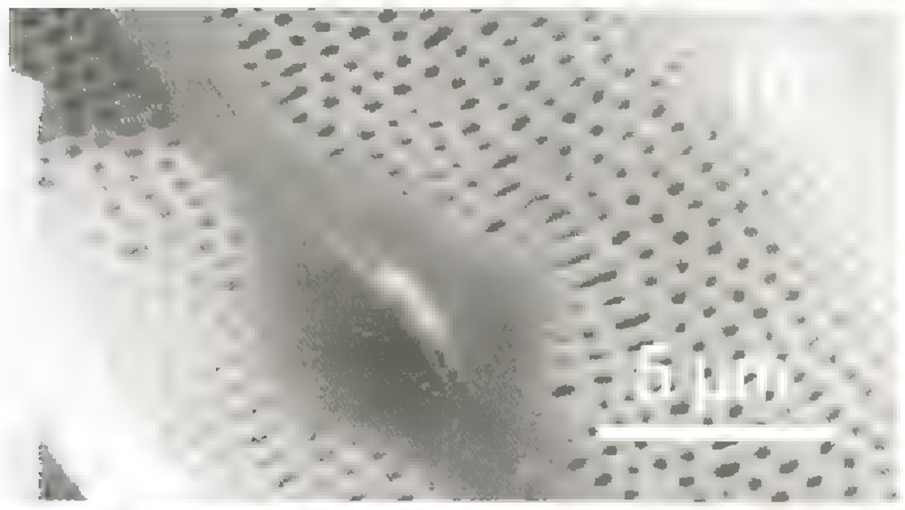
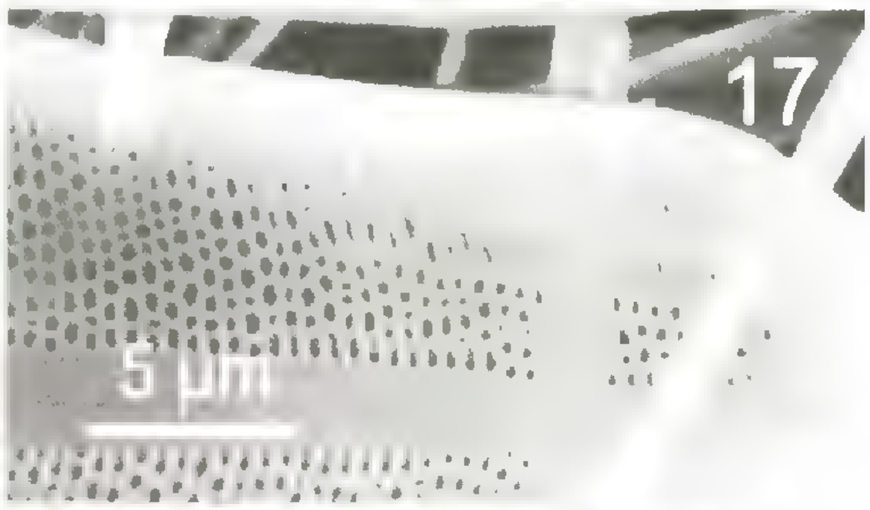
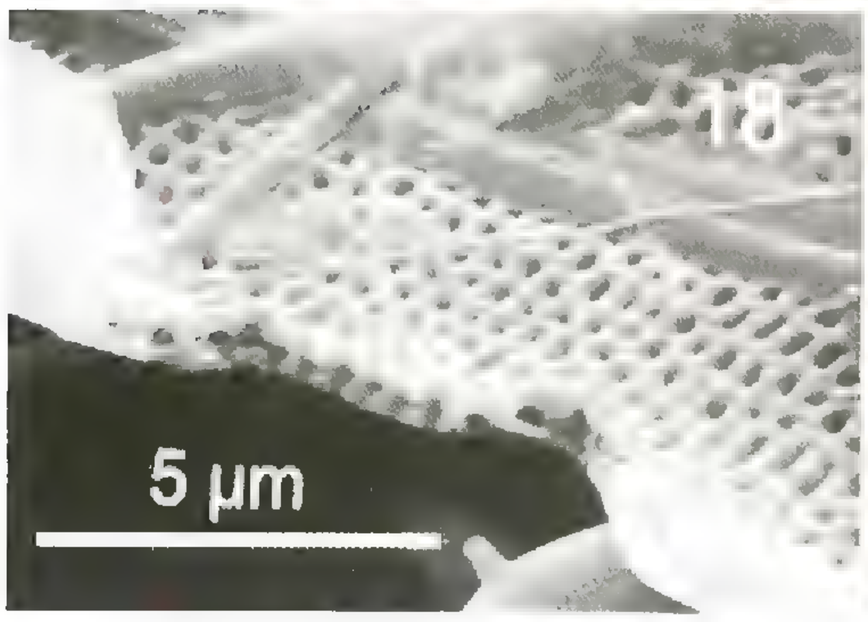
areolae along the mantle, the lacinia partially covers the terminal raphe ending. Note: on tilted specimens scale measures are subject to tilt error.

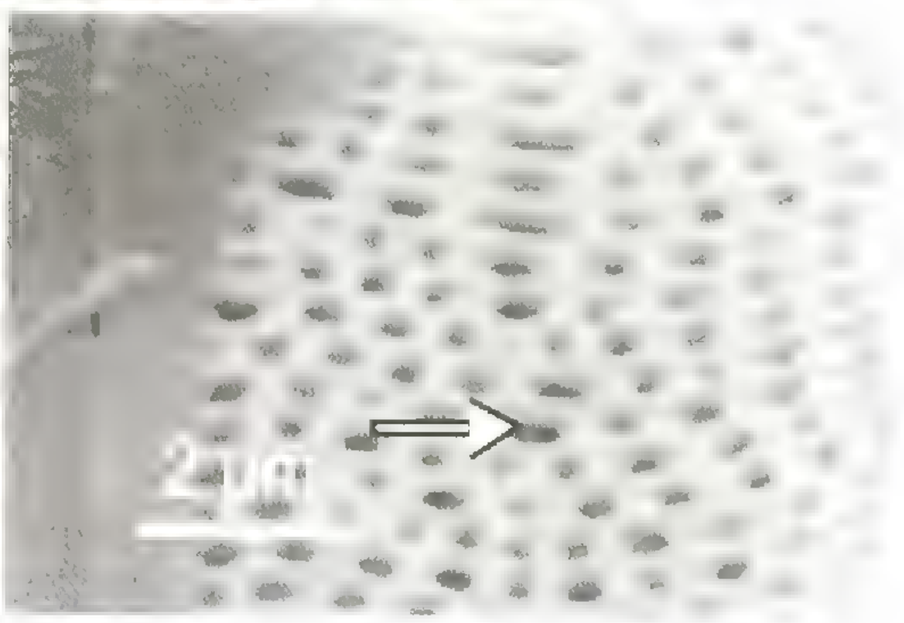












Figures 14–19. *Neidium rudimentarum*, SEM, internal surface valve structure. 14. Major proportion of valve, with large round areolae. 15. Apex showing the rudimentary canal and large elliptical openings; insert highlights the helictoglossa. 16. Central nodule, areolae slit-like around the central area with bimodal formation created by two adjacent helictoglossae. 17. Apex, internal valve projection, termination of the longitudinal canal is clearly visible. 18. Broken valve illustrating the chambered nature of the areolae. 19. A depressed region around each areola (arrow). Note: on tilted specimens scale measures are subject to tilt error.

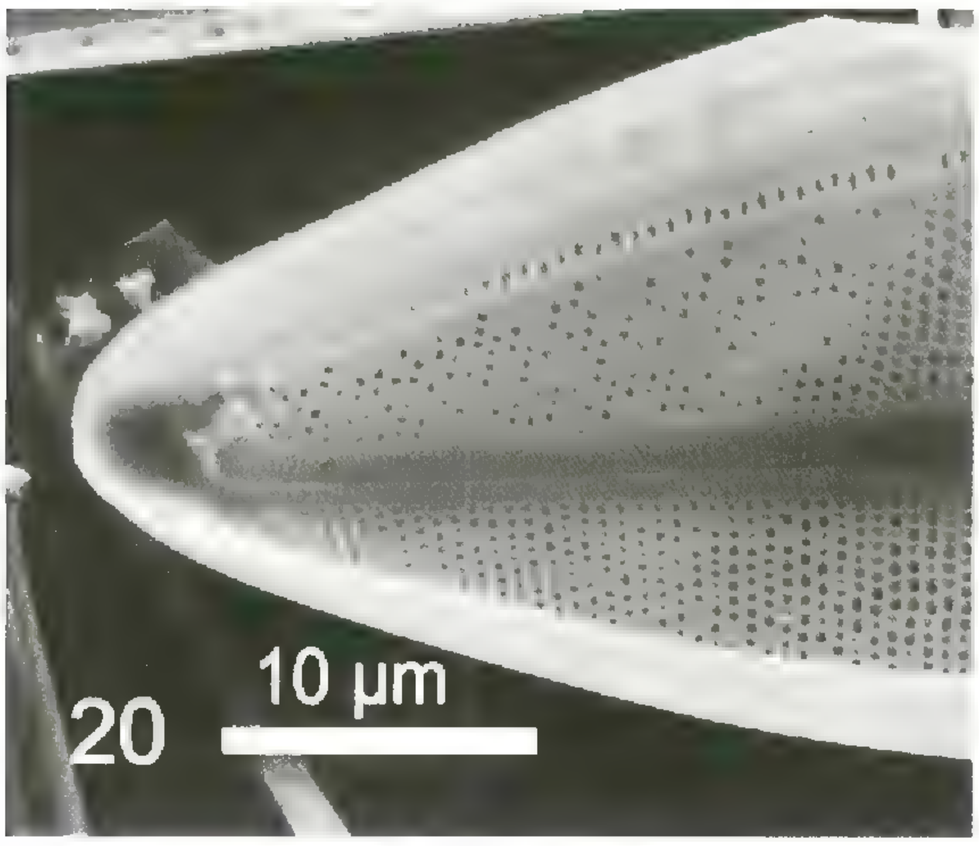
GEOLOGY AND ECOLOGY. The geology of the New Jersey Coastal Plain along the Great Egg Harbor River is Quaternary at the coastal outflow in Atlantic County to Upper Tertiary in the headwaters. The surficial sediments are generally sand and gravel deposits at Great Egg Harbor outflow to sand and green sands in the southern Gloucester County region. The local hydrogeology is a unique part of the Potomac-Raritan-Magothy Aquifer system (Gill and Farlekas 1976). The aquifer is productive in Gloucester and Camden Counties (ca. 50 billion litres of available water measured during 1967) and can be classified as a leaky artesian aquifer (Gill and Farlekas 1976).

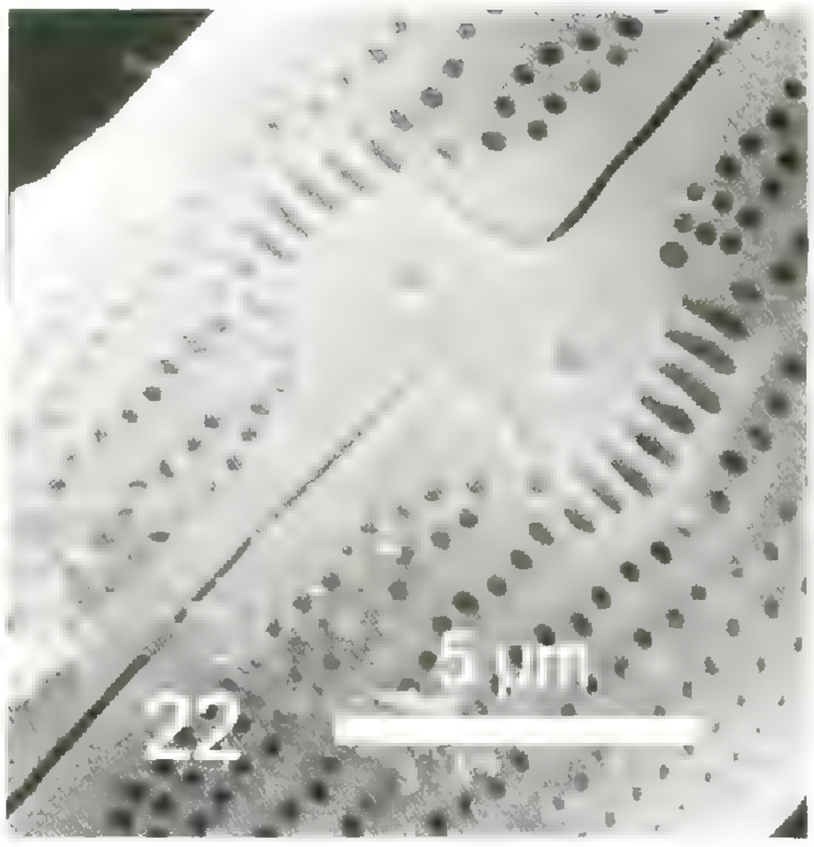
The Great Egg Harbor River flows from the headwaters within the Potomac-Raritan-Magothy aquifer system of the Winslow Wildlife Management Area (Gloucester County) to Great Egg Harbor Bay at Corbin City (Atlantic County), New Jersey. The river, west of Hanington and south of Berlin at Blue Hole pool is 15–25 m wide, and 1–2 m deep, with a predominantly sand cobble bottom. The original sample collected by T. C. Palmer lists the collection site as New Jersey, Winslow, Blue Hole, Inskip River. Although the site description is incomplete, the type locality is clearly Blue Hole (39°37.584′N, 74°53.279′W), located on the west side of Great Egg Harbor River within the Winslow Wildlife Management Area, immediately adjacent to Cecil Inskip Road.

A small article written in a local newspaper (author unknown) suggests that Blue Hole pool is an "ice" cold water pool, separated from the river by a 15 m bank, with the possibility of occasional spring flooding. Blue Hole pool is approximately 40–50 m long, 25 m wide and up to 3 m deep. The water is clear, with light easily penetrating to the bottom. The blue appearance of the water is enhanced by the reflection of light from the white diatomaceous earth and siliceous sediment at the bottom in the pool. The water analysed on October 27, 2003 was acidic (pH 4.3), with a low conductance (44 µS/cm). Allochthonous organic input to the pools (significant leaf accumulation within the near-shore zone) was clearly evident. Other taxa observed at this site of potentially poorly buffered oligotrophic water include *Asterionella* cf. *ralfsii* var. *americana* Körner, *Aulacoseira canadensis* (Hust.) Simonsen, *Brachysira neoacuta* Lange-Bert., *Eunotia zygodon* Ehrenb., *Frustulia rhomboides* (Ehrenb.) De Toni, *Neidium affine* (Ehrenb.) Pfitzer, *N. tumescens*, and *N. ampliatum*.

DISCUSSION

Longitudinal canals along the valve margin are the defining morphological structures for the genus *Neidium*. These canals can vary from one to >10 parallel chambers running along each margin (Figures 21, 22, 23). Single canals can be large and elevated like a keel (e.g., *N. hitchcockii*, *N. gracile*) or small within the valve silica matrix and hard to distinguish from adjacent areolae [e.g., *N. coralieae* Metzeltin & Krammer, *N. catariense* (Krasske) Lange-Bert.]. *Neidium rudimentarum* uniquely lacks a single complete longitudinal canal. Although not complete, this rudimentary canal is easily visible with a morphological structure similar to *N. ampliatum* and *N. hamatum* Metzeltin & Krammer





Figures 20–23. Some *Neidium* species highlighting differences among the taxa. 20. *Neidium ampliatum*. 21. *Neidium hamatum*, similar in morphology with a complete longitudinal canal from apex to apex. 22. *Neidium bergii* with lineate areolae around the central area. 23. *Neidium tumescens*, illustrating the presence of multiple canals adjacent to each other along the margin.

(Figures 20, 21). The areolae are also distinct slits on the external valve face whereas all other known species identified by SEM exhibit simple poroid to elaborate volae-covered areolae (Hamilton et al. 1995, 1996; Metzeltin and Lange-Bertalot 1998; Siver et al. 2003). Even though it lacks a complete canal and rounded externally opening areolae, this taxon clearly belongs within the genus because it contains other typical characters including the presence of deflected proximal raphe endings and laciniae at the apices. In general outline, two taxa are similar to *N. rudimentarum*: *N. hamatum* and *N. ampliatum sensu lato*. However these both have a well-developed complete longitudinal canal along each margin. The almost identical morphology of *N. hamatum* is especially interesting because this taxon is reported as a fossil in the Amazon, Brazil, and it may have some association with *N. rudimentarum*, which is an isolated endemic species less than 4,000 km to the north (Figure 21). The slit-like areolae around the central area and the undulating appearance of the areolae from apex to apex are also similar to structures observed in *N. bergii* (A. Cleve) Krammer (Figure 22). The significance of this similarity is not clear. Ecologically, *N. rudimentarum* is similar to most *Neidium* species preferring low pH, low conductance, and an organically rich benthic habitat.

The genus *Neidium* covers a large morphological range of canal types from one rudimentary canal (*N. rudimentarum*) to >10 well-developed canals (*N. tumescens*, Figure 23). The diversity of forms within the genus and the morphological variability of the species may have some implications in understanding the significance of longitudinal canals and keels which are observed in many genera within the Bacillariophyceae, both marine and freshwater.

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TWO NEW SPECIES AND ONE NEW NAME IN THE GESNERIACEAE FROM COSTA RICA

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ABSTRACT. Two new species of Gesneriaceae from the Caribbean slope of Costa Rica from the genera *Paradrymonia* and *Nautilocalyx* are described and illustrated. A new name in *Nautilocalyx* is proposed for *P. bullata* and a full description is provided.

Key Words: *Paradrymonia*, *Nautilocalyx*, Gesneriaceae, Mesoamerica, Costa Rica

Preparation of the treatment of the Gesneriaceae for the *Manual de Plantas de Costa Rica* project has revealed a new species of *Nautilocalyx* Linden *ex* Hanstein and one of *Paradrymonia* Hanstein from the Caribbean slope of Costa Rica. *Nautilocalyx* greatly resembles the genus *Paradrymonia* and differences stated by Hanstein (1853) in the original description provide no diagnostic characters for distinguishing these two genera. However, in recent works (Kvist et al. 1998; Skog 1979), *Paradrymonia* has been separated from *Nautilocalyx* by differences in habit (epiphytic vs. terrestrial), stem length in relation to leaf length (stems shorter than leaves vs. longer), anisophylly (strongly anisophyllous vs. isophyllous to subisophyllous), and inflorescence features (flowers congested vs. not congested).

Nautilocalyx is a neotropical genus of approximately 50 species characterized by its terrestrial habit, erect stems, showy corollas, and fleshy capsules. Only one species was previously known from Costa Rica, *N. dressleri* Wiehler.

Nautilocalyx purpurascens Kriebel, *sp. nov.* TYPE: COSTA RICA. Limón: Cordillera de Talamanca, Fila Matama, Cerro Muchilla, 9°47′40″N, 83°06′30″W, 850 m, 8 Apr 1989, *R. Robles 2704* (HOLOTYPE: INB!; ISOTYPES: MO, US). Figure 1.

A *Nautilocalyx punctatus* cui affinis, petioli 5–8 cm longis, foliis glabris vel puberulis, nectarii glandulae 2 opposita differt.

Terrestrial, perennial, herb to subshrub; stems unbranched, subquadrate, glabrous, erect, to 40 cm tall, ca. 5 mm in diameter, the internodes

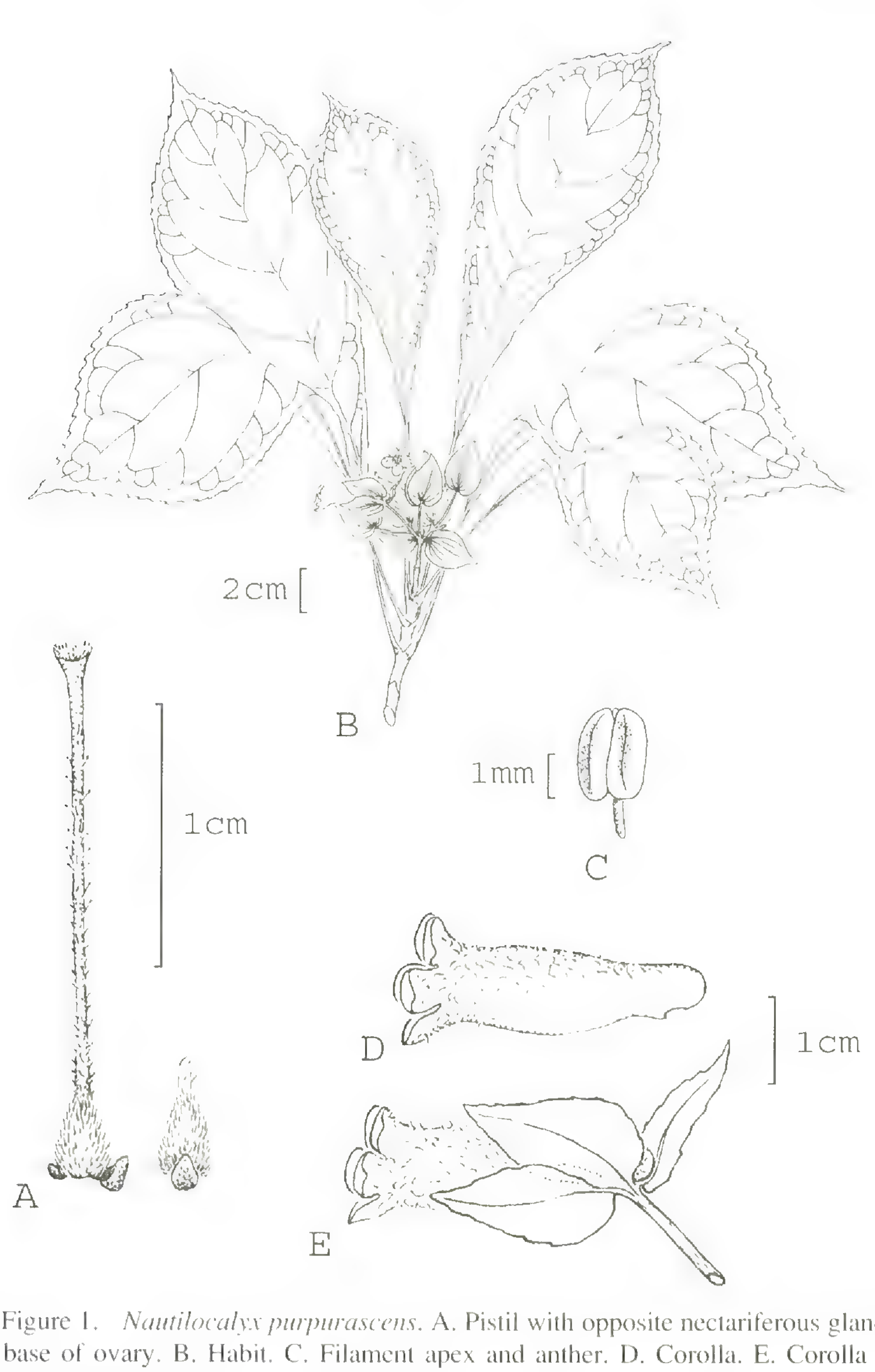

Figure 1. *Nautilocalyx purpurascens*. A. Pistil with opposite nectariferous glands at base of ovary. B. Habit. C. Filament apex and anther. D. Corolla. E. Corolla in calyx (*R. Robles 2704*).

1–3 cm long, rarely with adventitious roots in the lower nodes; leaf pairs equal to subequal, the petioles 5–8 cm long, fleshy, green flushed with purple, glabrous to puberulous, the lamina 13–20 (30) × 4–6 (10) cm, elliptic to oblanceolate, basally acute to attenuate on the petiole, apically

acuminate, serrate, membranous, green above, purple below, glabrous to sparsely puberulous on both surfaces, the lateral pairs of veins 8–11. Inflorescence axillary, cymes of 5–10 flowers, the peduncle 5–10 mm long, the prophylls and subtending bracts 15–25 × 9–21 mm, ovate, serrulate, similar to the calyx lobes, green to light purple, puberulous, the pedicels 5–20 mm long; calyx lobes 5, equal, 20–25 × 10–13 mm, lanceolate-ovate, membranous, connate for 1–2 mm, acuminate, serrate, green to light purple, puberulous; corolla 3–3.5 cm long, oblique in the calyx, infundibular, the spur ca. 2 mm long, glabrous to puberulous, the proximal half a narrow tube, white, sparsely pilose above, glabrous below, distal half gradually expanding, white, sparsely pilose on both sides, the lobes 5, subequal, ca. 10 × 7 mm, entire to crenulate, the inside and especially the entrance of the tube purple spotted, dorsally with short glandular hairs; stamens 4, included, the filaments adnate for 4 mm to the base of the corolla tube, ca. 2 cm, glabrous, the anthers coherent, each theca 2 × 1.8 mm, the theca dehiscing by longitudinal slits; ovary 3 mm long, sericeous, the style ca. 2 cm long, glandular pilose, the stigma stomatomorphic; disc composed of two opposite nectariferous glands, the ventral gland smaller, 0.5 × 0.3 mm, the dorsal gland larger, 1.5 × 1 mm, both glabrous. Capsule not seen.

DISTRIBUTION AND ECOLOGY. This species is known only from three specimens in the type locality, in riparian habitat, at 800–900 m. Specimens from Panama may also represent the same species (*fide* Skog).

ETYMOLOGY. The specific epithet refers to the usually purple stems, petioles, and abaxial surface of the leaf blade as well as the purple-spotted corolla of this species.

Nautilocalyx purpurascens is easily distinguished from its congeners by its glabrous to puberulous and usually purple stems, petioles, leaf underside and calyx, its purple-spotted corolla, and disc with two opposite nectariferous glands. The purple-spotted corolla of *N. purpurascens* most closely resembles that of *N. punctatus* Wiehler from Amazonian Venezuela from which it differs mainly by having glabrous to puberulous vegetative parts, much longer petioles, and a disc with two opposite nectariferous glands instead of a single dorsal gland.

PARATYPES. COSTA RICA. Limón: Cordillera de Talamanca, Fila Matama, Cerro Muchilla, 9°46′50″N, 83°05′30″W, 850 m, 5 Apr 1989, *R. Robles 2655* (INB, MO, US); Cordillera de Talamanca, Fila Matama, Cerro Muchilla, 9°47′40″N, 83°06′30″W, 850 m, 8 Apr 1989, *R. Robles & A. Chacón 2719* (INB, MO, US).

Nautilocalyx biserrulatus Kriebel, *nom. nov. Paradrymonia bullata* Gómez-Laur. & Chavarría, Brenesia 33: 145–147, 1990 [1991]. TYPE: COSTA RICA. San José: Tarrazú, 10 Feb 1988, *J. Gómez-L. 11686* (HOLOTYPE: CR!; ISOTYPES: F, USJ); non *N. bullatus* (Lem.) Sprague, Bull. Misc. Inform. Kew 1912: 89. 1912.

This species was originally described when only a few specimens were available for examination. Further explorations in the southern Pacific lowlands and middle elevations of Costa Rica have produced ample material. In order to better characterize the species, a full description is provided here.

Terrestrial, perennial, herbs to subshrubs; stems unbranched, villous, reddish, erect or ascending, to 40 cm tall, ca. 6 mm in diam., the internodes 8–20 mm long, sometimes with adventitious roots, when present generally in basal nodes; leaf pairs equal, subequal to rarely unequal, the petioles (2) 3.5–6 cm long, brownish, villous, the lamina elliptic to oblanceolate, 10–18 (24) × 3–6.5 cm, base acute, apex acuminate, margin biserrate, membranous, green and bullate on both sides, glabrescent to villous above, strigose to villous below, the lateral pairs of veins 9–11. Inflorescence axillary cymes of 2–5 flowers, the peduncle reduced or absent, the prophylls and subtending bracts linear to lanceolate, ciliate to serrulate, glabrate to villous, to 25 mm long, green, the pedicels 5–15 mm long; calyx lobes 5, equal, 17–21 × 1–2 mm, lanceolate to linear-lanceolate, membranous, free to the base, acuminate, biserrate, green, puberulous to villous; corolla oblique in the calyx, infundibular, ca. 3 cm long, the spur ca. 2 mm long, villous, white, proximal half a narrow tube gradually expanding towards the limb, the lobes 5, subequal, ca. 8 × 6 mm, entire; stamens 4, included, the filaments ca. 17 mm, adnate for 3 mm to the base of the corolla tube, glabrous, the anthers coherent, each anther 1.5–1.2 mm, the thecae dehiscing by longitudinal slits; ovary 4 mm long, sericeous, the style ca. 2 cm long, glabrous, the stigma stomatomorphic; disc a single dorsal nectariferous gland, 1.5 × 1 mm, entire, glabrous. Capsule ovate.

The species is always a terrestrial herb or subshrub with conspicuous stems to 40 cm long, generally equaling or surpassing leaf length, as is typical of *Nautilocalyx*, the leaves are well spaced along the stem and do not form an agglomerate rosette like most species of *Paradrymonia*. The leaves were originally described as anisophyllous like a typical *Paradrymonia* but have actually proven to be isophyllous to subisophyllous as in *Nautilocalyx*. Although the inflorescence was originally described as congested on the upper part of the stems with flowers, with pedicels

up to only 10 mm, recent material shows that flowers are also borne on up to 4 nodes below the stem apex on pedicels that reach 15 mm in length, producing a non congested inflorescence as is common in *Nautilocalyx*. Although both *Nautilocalyx* and *Episcia* Mart. often have species with bullate leaves (as are those of the present species), only *Episcia* has stolons, lacking in this species. On these characters and those listed by Kvist et al. (1998) and Skog (1979) this species is best placed in *Nautilocalyx* (see Table 1).

ETYMOLOGY. The specific epithet refers to the double-serrate leaf blade margin of this species.

Paradrymonia ommata L. E. Skog from Bocas del Toro, Panama, is similar to *Nautilocalyx biserrulatus* in the following diagnostic characters: they are both terrestrial herbs with evident stems that equal or surpass leaf length, both usually have biserrate leaf margins, the leaves are evidently petiolate, vegetative parts are glabrate to sparsely villous, calyx lobes are linear to lanceolate, and they have similar-sized corollas. They differ in that *P. ommata* has usually longer bracts, 1–5 cm long, and a corolla with the purple eye and purple veins (vs. bracts to 2.5 cm and an entirely white corolla). I am reluctant at this time to determine if the species are conspecific or to transfer *P. ommata* to *Nautilocalyx* pending further collections of *P. ommata*, a species otherwise known only from the type.

SPECIMENS EXAMINED. COSTA RICA. Puntarenas: Rancho Quemado, 6 Feb 1991, *M. M. Chavarría 423* (INB); Corcovado Nacional Park, Fila Matajambre, 7 May 1994, *J. González 251* (INB); Fila Costena, Fila Cruces, Río Piedras Blancas, 8 Dec 1993, *M. Grayum 10626* (INB); Jiménez, Dos Brazos de Río Tigre, Cerro Mueller, 26 Aug 1990, *G. Herrera 4143* (INB, US); Corcovado Nacional Park, Cerro Rincón, 2 Aug 1990, *C. Morales 10* (INB); Rincón, Rancho Quemado, 26 Oct 1990, *F. Quesada 196* (INB). San José: Tarrazú, Faja Costena del Valle del Parrita, Cerro Nara, 26 Jul 1995, *M.M. Chavarría 910* (INB, US); Tarrazú, *J. Gómez-L. 11686* (CR); Tarrazú, Fila Bustamante, 18 Apr 1994, *V. Ramírez et al. 318* (INB, MO, US).

Paradrymonia is also a small neotropical genus with approximately 30 species. Costa Rica has a great diversity of species of the genus, with about 11 species, as a result of its proximity to the possible center of diversity of the genus in Panama (Kvist et al. 1998).

Paradrymonia alata Kriebel, *sp. nov.* TYPE: COSTA RICA. Limón: Cordillera de Talamanca, Cantón de Matina, 200 m aguas debajo de la confluencia de Quebrada Canabral con Río Barbilla, 10°00′10″N, 83°25′30″W, 100 m, 5 Nov 1988, *G. Herrera 2287* (HOLOTYPE: INB!; ISOTYPE: MO). Figure 2.

Table 1. Comparison of diagnostic features in the genera *Nautilocalyx* and *Paradrymonia* with those of *N. biserrulatus*.

Nautilocalyx	*Paradrymonia*	*N. biserrulatus*
Plants terrestrial	Plants generally epiphytic	Plants terrestrial
Stems evident, equaling or surpassing leaf length	Stems reduced or absent, usually forming a rosette	Stems evident, usually equaling or surpassing leaf length
Leaves isophyllous to subisophyllous	Leaves generally strongly anisophyllous	Leaves isophyllous to subisophyllous or rarely anisophyllous
Leaf blades generally bullate	Leaf blades generally not bullate	Leaf blades bullate
Leaf blade base generally acute or truncate	Leaf blade base generally attenuate to decurrent	Leaf blade base generally acute or truncate
Petiole generally evident	Petiole generally reduced or obscured by decurrent leaf base	Petiole evident
Inflorescence not congested in the leaf axils	Inflorescence usually congested in the leaf axils	Inflorescence congested or not in the leaf axils

A *Paradrymonia longipetiolata* cui affinis, foliis majoribus, attenuatis; calycis lobatis ovato-lanceolatis, puberulis differt.

Epilithic, perennial, rosulate herb; stems unbranched, subquadrate, strigillose, reddish, erect or ascending, to 10 cm tall, ca. 1 cm in diameter, internodes 5–9 mm long, with adventitious roots; leaf pairs equal to extremely unequal, the petioles 22–29 cm long, fleshy, winged, reddish, strigillose, the lamina 22–27 × 13–20 cm, ovate to ovate-oblong, basally truncate or rounded, apically acute to acuminate, serrate, membranous, green above, whitish below, puberulous on both surfaces, the lateral pairs of veins 11. Inflorescence of axillary cymes of 5–11 flowers, the peduncle reduced, the prophylls and subtending bracts ca. 9 × 1–2 mm long, linear to lanceolate, entire to ciliate, glabrate to puberulous, reddish, puberulous, the pedicels 1–5 cm; calyx lobes 5, subequal, 20–25 × 5–11 mm, lanceolate-ovate, membranous, connate for 1–3 mm, acuminate, ciliate to serrulate, green with red or magenta base and occasionally longitudinal streaks, puberulous; corolla ca. 5 cm long, oblique in the calyx, infundibular, the spur ca. 5 mm long, glabrous to puberulous, proximal half a narrow tube, white, sparsely

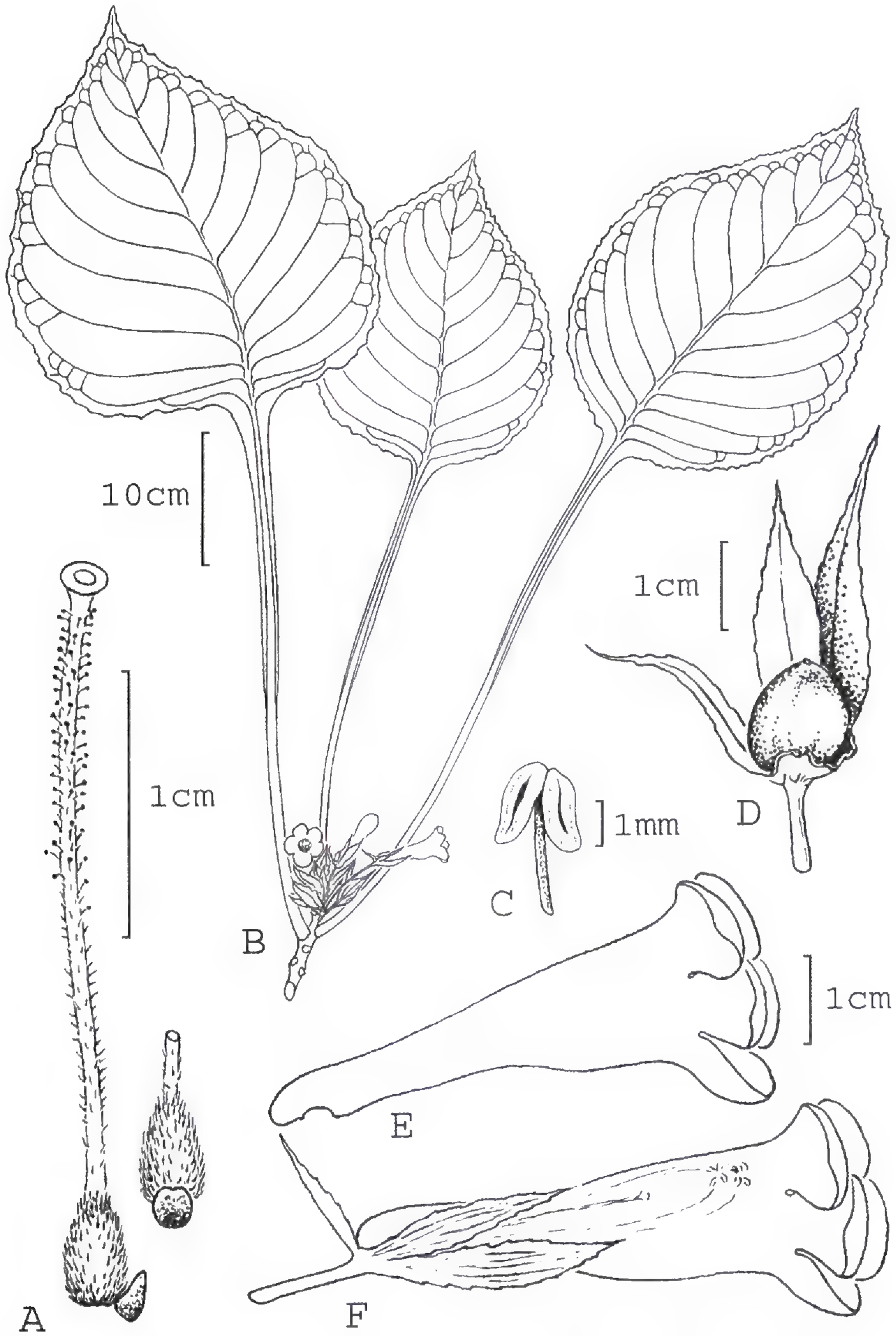

Figure 2. *Paradrymonia alata*. A. Pistil with dorsal nectariferous gland at base of ovary. B. Habit. C. Filament apex and anther. D. Capsule in calyx. E. Corolla. F. Corolla in calyx (*G. Herrera 2287*).

pilose above, glabrous below, distal half gradually expanding, white, occasionally with inconspicuous yellowish or reddish hues inside the tube, sparsely pilose on both sides, the lobes 5, subequal, ca. 13 × 11 mm, entire, the dorsal part of the tube inside with short glandular hairs; stamens 4, included, somewhat didynamous, ca. 4 cm, the filaments adnate for 6 mm to the base of the corolla tube, glabrous, each anther apically coherent to its homologous pair, each theca 2 × 1.8 mm, the thecae dehiscing by longitudinal slits; ovary 3 mm long, sericeous, the style ca. 3 cm long, densely glandular-pilose, the stigma capitate; disc of a single double-connate nectariferous dorsal gland, 1.5 × 1 mm, entire, glabrous. Fruit an ovate, bivalved, fleshy, white, glabrous capsule; seeds fusiform, 0.5 × 0.25 mm, dark brown when dry, finely striate.

DISTRIBUTION AND ECOLOGY. This species is known only from the Caribbean slope of Costa Rica in the Hitoy-Cerere Biological Reserve and Barbilla National Park from 50–250 m where it occurs in very wet forest.

ETYMOLOGY. The specific epithet refers to the winged petiole of this species.

Paradrymonia alata is characterized by its large leaves with long-decurrent leaf base and winged petiole, its lanceolate-ovate puberulous calyx lobes almost free to the base, and its large corollas up to 5 cm long. It is similar to the higher elevation *P. longipetiolata* (Donn.Sm.) Wiehler, which has smaller leaf blades with acute bases and linear to linear-lanceolate and densely pilose calyx lobes. It is also similar to *P. macrophylla* Wiehler, which has pedicels 8–11 mm long, the 2 lateral and 2 lower calyx lobes connate for ca. 1.6 cm, and the corolla wine-red to maroon-red spotted (vs. pedicels 1–5 cm long, calyx lobes free almost to the base, and an entirely white corolla with occasional yellowish or reddish hues inside the tube in *P. alata*).

PARATYPES: COSTA RICA Limón: Cordillera de Talamanca, Reserva Biológica Hitoy-Cerere, Valle del Río La Estrella, 9°38′55″N, 83°03′10″W, 200 m, 9 Feb 1989, *G. Herrera et al. 2367* (INB, MO); Cordillera de Talamanca, Cantón de Matina, Quebrada Canabral, 10°02′00″N, 83°24′30″W, 100 m, 8 Apr 1989, *M. Grayum et al. 8881* (INB, MO, US).

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NEW ENGLAND NOTE

REDISCOVERY OF *CAREX TYPHINA* (CYPERACEAE) IN MAINE

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Carex typhina Michx. is a perennial sedge of open and forested wetland communities. It belongs to the section *Squarrosae* Carrey, a group recognized by persistent styles and thin-walled, inflated, abruptly tapered perigynia with bidentate beaks (Gleason and Cronquist 1991). Though found throughout much of the eastern United States, *C. typhina* is rare in northern New England (Eastman 1978; Sorrie 1985; Vermont Nongame and Natural Heritage Program 1996). It ranges north to Essex County, Massachusetts and then is disjunct to southwestern Maine (Seymour 1982).

Bean (1942) was first to report *Carex typhina* in Maine. He collected the sedge in Leeds, Androscoggin County, from the shore of Wayne Pond (now referred to as Androscoggin Lake) in 1940 (*R. Bean 36826*, MAINE). Bean reported two stations of the plant along the "Cape," the delta where the Dead River meets the northwest shore of Androscoggin Lake. *Carex typhina* has not been reported from Maine since its initial discovery and was subsequently ranked SH (i.e., historically occurring and not reported for more than 20 years) by the Maine Natural Areas Program (1999).

On 16 July 2002, during a field trip for the Josselyn Botanical Society's 102nd meeting, we discovered a single plant of *Carex typhina* growing in a lacustrine floodplain forest on the northwest shore of Androscoggin Lake. Further survey effort yielded additional plants approximately 200 m from the initial discovery location. James Goltz and Candice McKellar observed a larger colony of *C. typhina* along the reverse delta of the Dead River. A voucher specimen was collected from this population.

SPECIMEN CITATION: U.S.A. Maine: Androscoggin Co., Leeds, floodplain forest along outlet delta of Androscoggin Lake, associated species: *Acer saccharinum*, *Carex intumescens*, *C. lupulina*, *Onoclea sensibilis*, and *Nyssa sylvatica*, 16 Jul 2002, *J. Goltz s.n.* (MAINE).

During a return trip, the primary author observed over 235 flowering individuals of *Carex typhina* on 30 July 2002. The plants were distributed over approximately 2.5 square kilometers in 32 subpopulations. Global Positioning System coordinates of the different colonies confirmed the population spanned into Wayne, Kennebec County. This represents a new county record for *C. typhina*. A second collection was taken to voucher this location.

SPECIMEN CITATION: U.S.A. Maine: Kennebec Co., Wayne, floodplain forest along outlet delta of Androscoggin Lake, associated species: *Acer saccharinum*, *Carex intumescens*, *C. lupulina*, *Onoclea sensibilis*, *A. rubrum*, and *Quercus rubra*, 22 Jul 2002, *M. Arsenault s.n.* (MAINE).

Carex typhina was most abundant along the delta of the Dead River and became very sparse within the lacustrine floodplain forest to the south of the delta. This vernally flooded area had a canopy dominated by *Acer saccharinum* L., *A. rubrum* L., *Fraxinus pennsylvanica* Marshall, and *Quercus rubra* L. Of note is that a few trees of *Nyssa sylvatica* Marshall, a species uncommon in Maine, were occasional in this plant community. The shrub layer consisted primarily of *Lyonia ligustrina* (L.) DC., *Spiraea tomentosa* L., and *Viburnum dentatum* L. var. *lucidum* Aiton. Common herbs included *C. intumescens* Rudge, *Onoclea sensibilis* L., *Osmunda regalis* L. var. *spectabilis* (Willd.) A. Gray, *O. claytoniana* L., *C. lupulina* Muhl. *ex* Willd., *C. projecta* Mack., *C. scoparia* Schkuhr *ex* Willd., *Iris versicolor* L., *Apios americana* Medik., and *Uvularia sessilifolia* L.

Conservation of *Carex typhina* in New England should be of high priority due to its regional rarity. In Maine, this species was found to inhabit a natural community with an unusual hydrologic regime on privately owned land. The high volume of melt water from the Androscoggin River forces the Dead River to reverse its flow in the spring (i.e., it changes from an outlet to an inlet), subsequently flooding the delta and neighboring habitats on Androscoggin Lake. A dam has been installed on the Dead River with flashboards that close when the flow of the river is reversed, reducing the severity of flood events. There is current pressure on part of the Androscoggin Lake Improvement Corporation to improve the dilapidated condition of the flashboards to further reduce vernal flows into the lake in an effort to improve water quality (Saunders 2001). Research is currently underway to ascertain the effect of minimizing spring flood events on *C. typhina* and associated natural communities (Karol Worden, Woodlot Alternatives, pers. comm.) and to monitor the population over several years (Theresa Kerchner, Androscoggin Lake Improvement Corp, pers. comm.).

ACKNOWLEDGMENTS. We thank the Josselyn Botanical Society, Theresa Kerchner, and Karol Worden.

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NEW ENGLAND NOTE

DRABA GLABELLA (BRASSICACEAE), NEW TO MAINE

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Draba L. is a large genus of low, annual to perennial herbs distributed nearly worldwide (Rollins 1993). Three species of native New England *Draba* form a morphologically and ecologically similar group—*D. arabisans* Michx., *D. breweri* S. Watson var. *cana* (Rydb.) Rollins, and *D. glabella* Pursh. All three species are perennials with a well-developed caudex and have reproductive stems with 3 or more leaves, basal leaves with stellate hairs, white petals, and compressed silicles (Mulligan 1976; Rollins 1993). They are inhabitants of high pH bedrock cliffs, talus slopes, and rocky woodlands. Further, within New England, all three species are restricted to northern states (i.e., Maine, New Hampshire, and Vermont; Seymour 1982). The species are often misidentified, in large part due to over-reliance on non-diagnostic characters in botanical manuals (see below). Herbarium surveys of regional museums for the Herbarium Recovery Project, administered by the New England Wild Flower Society, have altered the known distribution of *D. glabella* in New England. This note presents a new record for *D. glabella*, discusses excluded locations, and presents a regional key.

Draba glabella (synonyms: *D. daurica* DC.; *D. arabisans* var. *orthocarpa* Fernald & C. H. Knowlt.) is a circumpolar species that displays a wide range of morphologies in response to edaphic factors (Rollins 1993). It is closely related to *D. arabisans* and the two species have been combined (Boivin 1966). However, Mulligan (1970) presented morphological, geographical, and cytological evidence for recognition of both species. In New England, *D. glabella* has been previously reported only from Vermont (Seymour 1982).

Northern New England specimens of *Draba* from CONN, GH, HCOA, MAINE, MASS, NEBC, NHA, NUV, SMCW, and VT were critically examined using morphological characters stressed by Mulligan (1970, 1976; see below). A new location for *D. glabella* was discovered from Mount Kineo, Kineo Township, Maine. Identification of specimens from NEBC were confirmed by Ihsan Al-Shehbaz (Missouri Botanical Garden).

SPECIMEN CITATION: U.S.A. Maine: Piscataquis Co., Kineo Township, base of cliff at Mt. Kineo, *unknown collector s.n.* (MAINE); Mt. Kineo, base of cliff, 6 Jun, *F. Bunker s.n.* (MAINE); Mt. Kineo, on dry, calcareous ledges and soils, E cliff, growing with *Potentilla recta* and *Arabis glabra*, 20 Aug 1986, *S. Rooney, B. Bochan & G. Morse 101* (MAINE); Mt. Kineo, E face, moist calcareous ledges, with *Primula laurentiana* and *Carex capillaris*, 12 Jul 1992, *H. Hinds s.n.* (MAINE); Mt. Kineo, 21 Sep 1887, *G. Kennedy s.n.* (NEBC); Mt. Kineo, S lower cliffs, rock shelves, 31 Aug 1 Sep 1907, *J. Cushman 1894* (NEBC); Mt. Kineo, base of cliff, 1878, *M. Fernald s.n.* (MASS).

Mount Kineo is a small peak rising to 550 m elevation in central Maine. It occurs on an exposed peninsula extending out from the east shoreline of Moosehead Lake. Mount Kineo is well known for its northern and/or calciphilic flora, including *Agrostis mertensii* Trin., *Carex aurea* Nutt., *C. capillaris* L., *Clematis occidentalis* (Hornem.) DC., *Dryopteris fragrans* (L.) Schott, *Epilobium ciliatum* Raf. subsp. *ciliatum*, *Trisetum melicoides* (Michx.) Vasey *ex* Scribn., and the only known extant inland population of *Primula laurentiana* Fernald in New England. This list of species seems unusual given that the bedrock is Kineo Rhyolite, a flint-like volcanic rock that was laid down during violent eruptions of steam and ash (Caldwell 1998). Rhyolite, which has high silica content, would be expected to be a relatively acidic rock (George Kendrick, Woodlot Alternatives, Inc., pers. comm.). However, at Mount Kineo the rhyolite overlays the Tarratine Formation, a sandstone created during Devonian times with abundant fossils and, therefore, an ample supply of calcium (Caldwell 1998; Osberg et al. 1985). Mount Kineo has exposed cliffs on the south and east faces of the mountain. *Draba glabella* occurs there along the base of the cliffs, often in partial shade of *Thuja occidentalis* L.

Review of specimens in regional herbaria shows that *Draba glabella* and *D. arabisans* are frequently misidentified. Confusion between these two species is primarily due to use of non-diagnostic characters for determination. Fernald (1934, 1950), for example, utilized cauline leaf shape, pedicel thickness and length, and silique morphology, among other characters, to discriminate between *D. arabisans* and *D. glabella*. All of these characters overlap and do not lead to reliable identification of the species. Modern regional manuals emphasize flat versus twisted siliques as an important character (Gleason and Cronquist 1991; Magee and Ahles 1999). This character too cannot be used as a sole criterion for determination (specimens of *D. glabella* from Mount Kineo frequently have twisted fruits contrary to statements in modern manuals).

Mulligan (1970, 1976) stressed the importance of trichome morphology for separation of *Draba arabisans* and *D. glabella*. *Draba*

arabisans has sessile stellate hairs on the abaxial (i.e., lower) surfaces of the basal leaves. At 20× magnification, the radiating branches of the hairs can be seen to lie flat on the blade surface. *Draba glabella*, on the other hand, shows short-stalked stellate hairs on the abaxial surfaces of basal leaves. Viewed at magnification, the radiating branches of the hairs are elevated above the leaf surface. Comparative images of trichomes of *Draba* can be found in Mulligan (1976). Caution: poorly pressed specimens of *D. arabisans* in many instances appear to have stalked stellate hairs due to irregular drying and dimpling of the leaf surface (this artificially lifts the branches of the hairs above the blade surface). Be sure to view the trichomes at an angle parallel with the leaf surface to correctly determine the presence or absence of stalks.

Mulligan (1970, 1976) and Rollins (1993) also utilized style length as a diagnostic character for separation of *Draba arabisans* and *D. glabella*. Both authorities state in the identification keys that *D. arabisans* has styles longer than 0.25 mm and *D. glabella* has styles shorter than 0.25 mm. Review of New England collections indicates that style length, though useful, will not work for some plants (specimens of *D. glabella* from Maine and Vermont have styles up to 0.4 mm long).

Prior to the discovery of *Draba glabella* from northern Lake Champlain shoreline bluffs (e.g., Sunset Island, *P. Zika 5165*, VT; Providence Island, *P. Zika 9185*, VT), the species had previously been reported from Salisbury (Mt. Moosalamoo) and Westmore (Mt. Pisgah), Vermont, in New England (Dole 1937; Seymour 1982). These latter records were based on misidentified specimens of *D. arabisans* and were annotated as such during herbarium surveys for the Herbarium Recovery Project. The two specimens collected by Peter Zika were confirmed as *D. glabella* by Ihsan Al-Shehbaz (Missouri Botanical Garden). In summary, the verified New England distribution of *D. glabella* includes Grand Isle and Chittenden Counties, Vermont, and Piscataquis County, Maine.

KEY TO NEW ENGLAND *DRABA*

1. Petals bilobed with a deep, apical sinus; stems scapose (i.e., all the leaves confined to a basal cluster) . . . . . *D. verna*
1. Petals entire or emarginate at apex; stems with at least 1 leaf-bearing node 2
   2. Plants annual; rachis of infructescence congested, 1–16 (–35) mm long; stem leaves all borne at base just above the basal rosette of leaves . . . . . *D. reptans*

2. Plants perennial from a caudex; rachis of infructescence relatively elongate, (16–) 20–78 mm long; stem leaves more evenly distributed, usually some produced in the apical half of the stem 3
3. Lowest 1–3 flowers each subtended by a leafy bract; siliques pubescent with stellate hairs . . . . . *D. breweri*
3. None of the flowers subtended by leafy bracts; siliques glabrous or sparsely pubescent with simple or forked hairs 4
4. Stellate hairs of abaxial surface of basal leaves borne on short stalks, the radiating branches of the hairs elevated above the surface of the leaf blade; styles up to 0.3 (–0.4) mm long; stigmas often bilobed . . . . . *D. glabella*
4. Stellate hairs of abaxial surface of basal leaves sessile, the radiating branches of the hairs appressed to the leaf surface; styles (0.3–) 0.4–1 mm long; stigmas scarcely bilobed . . . . . *D. arabisans*

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NEW ENGLAND NOTE

NOTEWORTHY PLANTS IN CREATED WETLANDS IN SOUTHEASTERN NEW HAMPSHIRE

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During the summer of 2002 a floristic study was conducted of four created wetlands. One site (PORTS) in Portsmouth, New Hampshire, was a 13-acre wetland created in an abandoned gravel pit adjacent to a Conservation Commission protected parcel of land, enhancing its value as a conservation easement (Normandeau Associates 1986; Padgett 1993). Padgett and Crow (Padgett 1993; Padgett and Crow 1994) carried out a floristic inventory of PORTS in 1992 during its 7th growing season, while the 2002 assessment evaluated the floristic changes during the interim 10 years and occurred in the 17th growing season.

The remaining three wetlands were created in Brentwood, New Hampshire as part of a large wetland complex and a multi-year mitigation effort carried out by the New Hampshire Department of Transportation (NHDOT) and implemented by Normandeau Associates, Inc. to replace wetlands lost through the expansion of Route 101 from a two-lane highway to a four-lane divided highway (Garlo et al. 1997). The floristic study of Southern Pond (SOUTH), created in 1995, occurred in its 8th growing season, while the other two wetlands, Northern Pond (NORTH) and Eastern Pond (EAST), created in 1998, were inventoried in their 5th growing season.

The procedures involved in the wetland creation may explain the presence of the rare species. All four created wetlands received transplanted muck soils from the impacted wetlands, containing seeds and vegetative propagules, as a top dressing and to aid in revegetation (Garlo 1992; Garlo et al. 1997; Normandeau Associates 1986). The muck soils may have contained seeds or propagules occurring in the impacted wetlands. Extensive plantings and wetland and upland seed mixes were procured for revegetation at NORTH, SOUTH, and EAST (Garlo et al. 1997; Normandeau Associates 1996, 1997). Unfortuately, the geographical origins of the seed mixes and plantings for the Brentwood wetlands remain unknown. Native shrubs from a preselected list of

species were also planted at PORTS, and the mitigation plan allowed for subsequent plantings from the list in the event of slow revegetation (Normandeau Associates 1986; Padgett 1993; Padgett and Crow 1994). However, records of the origin of these plantings and list of plants that were planted were not required under the mitigation plan and therefore were not kept. It is therefore recommended that careful records of seed and planting purchases be kept and that plant materials be purchased from nurseries within the region offering native species.

NEW STATE RECORD

Carex atherodes Spreng. (Wheat Sedge), found in PORTS, represents the first record of this species for New Hampshire. Despite a circumboreal global range (Dibble 2001), it is considered regionally rare in New England (Brumback and Mehrhoff, et al. 1996). Only two other extant populations of *C. atherodes* are known in New England, one in northwestern Vermont and one in coastal Maine (Dibble 2001), with other historical populations documented earlier than 1970 (Brumback and Mehrhoff, et al. 1996). Several sources refer to *C. atherodes* as typical of the flora of prairie wetlands and sedge meadows of the Midwest (Kirby et al. 1989; Van der Valk et al. 1999; Welling et al. 1988); it is a species often used as hay or forage (Kirby et al. 1989).

Carex atherodes was found on the southwestern side of the created wetland near the upland-wetland border. The plant was found growing in damp to wet soil of the *Juncus effuses–Phalaris arundinacea* cover-type vegetation, as recognized by Padgett and Crow (1994; Padgett 1993). Dibble (2001) noted the habitat for *C. atherodes* as being varied, including marshes exhibiting a stable hydrology, and stated that it is often associated with *P. arundinacea* L., as was the case at PORTS.

SPECIMEN CITATION: U.S.A. New Hampshire: Rockingham Co., Portsmouth, Route 1, created wetland, 12 Jun 2002, *K.J. Jahr 238* (NHA).

RARE SPECIES

The current *Plant Tracking List* of the New Hampshire Natural Heritage Bureau (2003) was used to determine whether any catalogued species in the created wetlands had special status in the state. *Flora Conservanda*, the list compiled by New England Plant Conservation Program (NEPCoP), was also consulted to assess each species' prevalence in the New England area as a whole (Brumback and Mehrhoff, et al. 1996).

Four species found in the study areas were listed as "endangered" for the state by the New Hampshire Natural Heritage Bureau (2003).

Glyceria acutiflora Torr. (Manna Grass) occurred in SOUTH with scattered abundance. Populations were growing in shallow water on the north and northwestern shores of the wetland.

SPECIMEN CITATION: U.S.A. New Hampshire: Rockingham Co., Brentwood, Pine Road, Southern Pond, 17 Jun 2002, *K.J. Jahr 301* (NHA).

Lindernia anagallidea (Michx.) Pennell (False Pimpernel) occurred in NORTH, SOUTH, and EAST, inhabiting mudflats exposed by receding water. Populations were common in NORTH and EAST, while occurring occasionally in SOUTH.

SPECIMEN CITATIONS: U.S.A. New Hampshire: Rockingham Co., Brentwood, Pine Road, Northern Pond, 27 Aug 2002, *K.J. Jahr 896* (NHA); Southern Pond, 26 Aug 2002, *K.J. Jahr 874* (NHA); Eastern Pond, 2 Aug 2002, *K.J. Jahr 751* (NHA).

Potamogeton foliosus Raf. (Leafy Pondweed) occurred in two sites, SOUTH and the larger depression of EAST. Populations in SOUTH were uncommon, only growing in shallow water at the northern end of the wetland. However, *P. foliosus* occurred as scattered masses just off the northern shore of the island in EAST. *Potamogeton foliosus* was reported as "frequent" abundance at PORTS by Padgett and Crow (1994), but was absent in the 2002 PORTS assessment.

SPECIMEN CITATIONS: U.S.A. New Hampshire: Rockingham Co., Brentwood, Pine Road, Southern Pond, 19 Jul 2002, *K.J. Jahr 686* (NHA); Eastern Pond, 15 Jul 2002, *K.J. Jahr 585* (NHA); Portsmouth, Route 1, created wetland, 1992, *D.J. Padgett 164* (NHA).

Rumex pallidus Bigelow (White Dock) was found at PORTS. The plant was uncommon and grew within the emergent zone along the wetland's southern side.

SPECIMEN CITATION: U.S.A. New Hampshire: Rockingham Co., Portsmouth, Route 1, created wetland, 3 Jun 2002, *K.J. Jahr 131* (NHA).

Two species encountered, *Epilobium ciliatum* Raf. subsp. *ciliatum* and *Sparganium eurycarpum* Engelm., have "threatened" status in the state of New Hampshire (New Hampshire Natural Heritage Bureau 2003).

Epilobium ciliatum subsp. *ciliatum* (American Willow-herb) occurred in PORTS, NORTH and EAST. Uncommon at PORTS, this species inhabited the wet meadow edge of upland islands. Occasional in abundance in one pond of NORTH, *E. ciliatum* subsp. *ciliatum* grew on wet sandy shores and wet soils just inland from the open water. The

populations in EAST were scattered and mainly in wet areas and muddy depressions where water had receded.

SPECIMEN CITATIONS: U.S.A. New Hampshire: Rockingham Co., Brentwood, Pine Road, Northern Pond, 1 Jul 2002, *K.J. Jahr 393* (NHA); Eastern Pond, 26 Jun 2002, *K.J. Jahr 346* (NHA).

Sparganium eurycarpum (Burreed) occurred only in the PORTS flora, and was reported by Padgett and Crow (1994). This rare species was reported as "common" and "frequent along the western edge of the wetland" by Padgett and Crow (1994), but was abundant and found growing in emergent zones, shallow depressions, and shallow canals throughout the wetland in 2002. *Sparganium eurycarpum* propagules or fruits may have been in the muck soils transplanted from the impacted wetlands, or may have been planted. Although it is native to the seacoast area, it was included on a list of potential plantings to be made at PORTS if the revegetation had not progressed satisfactorily during the first growing season (Normandeau Associates 1986), and therefore may have been planted early in the wetland's establishment. Monitoring reports were not required for the mitigation at PORTS, so detailed records of subsequent plantings do not exist, making determination of the origin of the rare plant material difficult.

SPECIMEN CITATIONS: U.S.A. New Hampshire: Rockingham Co., Portsmouth, Route 1, created wetland, 25 Jun 2002, *K.J. Jahr 331* (NHA), *D.J. Padgett 53, 81* (NHA).

Two species, *Isoetes engelmannii* A. Braun (Quillwort) and *Potamogeton nodosus* Poir. (Narrowleaf Pondweed), were included on the state tracking list, but had no current status indication.

Isoetes engelmannii was uncommon in NORTH and EAST, but scattered in SOUTH. It was typically found in shallow waters with sandy substrate bottoms in all three wetlands.

SPECIMEN CITATIONS: U.S.A. New Hampshire: Rockingham Co., Brentwood, Pine Road, Northern Pond, 12 Jul 2002, *K.J. Jahr 527* (NHA); Southern Pond, 10 Jul 2002, *K.J. Jahr 474* (NHA); Eastern Pond, 15 Jul 2002, *K.J. Jahr 595* (NHA).

Potamogeton nodosus was commonly growing in shallow water throughout SOUTH, especially in the southern section of the wetland. *Potamogeton nodosus* was reported to have been planted as over-wintering buds throughout aquatic zones in SOUTH, NORTH, and EAST (Normandeau Associates 1997), although it apparently became established only in SOUTH.

SPECIMEN CITATION: U.S.A. New Hampshire: Rockingham Co., Brentwood, Pine Road, Southern Pond, 10 Jul 2002, *K.J. Jahr 486* (NHA).

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NEW ENGLAND NOTE

INLAND SANDY ACID PONDSHORES IN THE LOWER CONNECTICUT RIVER VALLEY, HAMPDEN COUNTY, MASSACHUSETTS

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The flora and plant communities of coastal plain ponds are well known in Massachusetts, having been the subject of intensive field studies related to rare plant and habitat conservation for this distinctive natural community type. However, relatively little is known about inland pondshore vegetation in the Commonwealth (Swain and Kearsley 2000), possibly due to the requirement for sampling to coincide with suitable conditions (i.e., a protracted period of drought and resulting water level drawdown; an interval of a few to several years may pass before these conditions are optimum). Extended severe drought and low groundwater levels during the summer of 2002 afforded a unique opportunity to qualitatively survey the flora and plant communities of drawn-down exposed sandy pondshores at 13 sites in the Lower Connecticut River Valley, Hampden County, Massachusetts.

Surveys of ponds known to have, or suspected to have, areas of exposed sandy shores were conducted in the towns of Springfield, Longmeadow, Ludlow, and Wilbraham (Table 1). It should be noted that Lake Lorraine and Five Mile Pond are essentially the same pond, separated into two parts by a railroad embankment. The perimeter of each pond was surveyed on foot in order to identify areas of exposed sandy shores and to qualitatively assess plant species composition and community zonation in the immediate vicinity of the shore. Access to the larger water bodies was facilitated by the use of a canoe.

PHYSICAL FEATURES

The ponds were located within a 10-mile radius of Springfield, the largest city in a densely populated physiographic province of west-central Massachusetts known as the Connecticut River Valley Lowlands (Motts and O'Brien 1981). The area is distinguished by a low, broad, north–south river valley transected by linear basalt ridges with high relative relief. All of the ponds visited occurred in areas of deep, acidic, well drained to

Table 1. Location of survey sites, inland sandy acid pondshores, Hampden County, Massachusetts. (Latitude/longitude coordinates expressed in degrees.-minutes.seconds.)

Site	Town	Latitude	Longitude	Area (acres)	No. Species
Five Mile Pond	Springfield	42.08.30	72.30.40	36	81
Lake Lorraine	Springfield	42.08.44	72.30.50	27	69
Mona Lake	Springfield	42.08.33	72.31.16	11	75
Loon Pond	Springfield	42.08.36	72.29.57	29	62
Bass Pond	Springfield	42.06.25	72.30.07	12	45
Dimmock Pond	Springfield	42.08.56	72.29.27	10	72
Long Pond	Springfield	42.09.16	72.30.30	18	71
Spectacle Pond	Wilbraham	42.08.59	72.26.19	16	68
Longmeadow Pond	Longmeadow	42.02.03	72.32.29	6	53
Minechoag Pond	Ludlow	42.09.46	72.27.36	21	87
Gamache Pond	Ludlow	42.10.14	72.29.18	15	81
Haviland Pond	Ludlow	42.10.21	72.28.29	25	58
Murphy Pond	Ludlow	42.10.17	72.29.37	8	67

excessively drained coarse-textured glaciofluvial sediments associated with flat to gently sloping glacial outwash plains and terraces (Hartshorn and Koteff 1967). Several of the ponds occurred in kettlehole depressions. Soils in the area are dominated by the Hinckley-Windsor-Merrimac association (Mott and Swenson 1978). Regional vegetation is predominantly the pitch pine–oak type described by Westveld et al. (1956).

Pond size varied in area from as small as 6 acres to as much as 36 acres (Five Mile Pond, Springfield), with most ponds surveyed being around 18 acres in size (McCann and Daly 1972). However, the area of exposed sandy shoreline present varied greatly from site to site, and overall pond size was not necessarily proportional to the amount of sandy pondshore habitat present. The extent of exposed sandy substrate appeared to be largely determined by basin morphometry (i.e., basins with shallow, very gently sloping littoral areas tend to have more sandy substrate exposed following relatively small reductions in water level). The frequency, magnitude, and duration of drawdown may also influence the amount of exposed sandy substrate by hastening the decomposition (oxidation) of organic matter admixed with mineral sediment (Zaremba and Lamont 1993).

FLORA AND VEGETATION

One hundred twelve species of vascular plants were observed at the ponds during the course of the 2002 field survey (Appendix). Although

shoreline vegetation was not quantitatively sampled at any of the 13 sites, five easily discernible generalized vegetation zones separated on the basis of gross physiognomy and relative elevation position were present at most of the ponds; these zones correspond to those described for coastal plain ponds on Long Island, New York (Zaremba and Lamont 1993). Brief descriptions of the zones are given below, and are listed in order from the upland border to the pond interior. Nomenclature follows Gleason and Cronquist (1991). Voucher specimens have been deposited at Eastern Illinois University (EIU), the New England Botanical Club Herbarium (NEBC), and the University of Michigan (MICH).

Zone 1 – Wetland shrub and tree thicket at the upland border. Common trees include *Nyssa sylvatica* and *Acer rubrum*; common shrubs include *Cephalanthus occidentalis*, *Vaccinium corymbosum*, and *Alnus serrulata*. Other less common shrubs include *Myrica gale*, *Clethra alnifolia*, *Rhamnus frangula*, and *Lyonia ligustrina*.

Zone 2 – Tall herbaceous and graminoid species at or slightly above the approximate elevation of mean high water. Common elements include *Lythrum salicaria*, *Decodon verticillatus*, *Polygonum pensylvanicum*, *P. careyi*, *P. lapathifolium*, *P. sagittatum*, *Leersia oryzoides*, *Panicum dichotomiflorum*, *Echinochloa muricata* var. *muricata*, *Scirpus cyperinus*, *Epilobium ciliatum* var. *ciliatum*, *Verbena hastata*, *Bidens connata*, and *Eupatorium perfoliatum*. Plant height may reach as much as 4–6 feet in this zone, indicating probable persistence of individuals from year to year from surviving perennial rootstocks; stem densities are typically quite high. Most of the species listed for this zone are typical of eutrophic wetland environments, and probably reflect extraneous nitrogen inputs from developed residential areas on adjacent uplands.

Zone 3 – Low herbaceous species zone on predominantly sandy sediments exposed during seasonal or intermittent drawdown, typified by a great diversity of low, mostly annual, herbaceous and graminoid species. Included among the common species are *Cyperus dentatus*, *C. erythrorhizos*, *C. strigosus*, *C. bipartitus*, *C. squarrosus*, *Hemicarpha micrantha*, *Fimbristylis autumnalis*, *Rhynchospora capitellata*, *Juncus brevicaudatus*, *J. acuminatus*, *J. canadensis*, *J. pelocarpus*, *J. tenuis*, *Panicum rigidulum*, *Bidens cernua*, *Erechtites hieraciifolia*, *Gnaphalium uliginosum*, *Hypericum canadense*, *H. mutilum*, *Polygonum hydropiper*, *P. hydropiperoides*, *P. punctatum*, *Lycopus uniflorus*, *Lindernia dubia* var. *dubia*, *L. dubia* var. *anagallidea*, and *Agalinis purpurea* var.

purpurea. Density of vegetation in this zone varies from sparse cover to dense carpets of plants with little or no unvegetated sandy substrate. Species diversity per unit area is also typically quite high; as many as 15 species were noted within a one square yard area at Minechoag Pond, Ludlow. However, species composition in this zone is highly variable from site to site, and as noted by Zaremba and Lamont (1993), there may be great variability in composition from year to year. Due to the semi-permanently flooded hydrologic regime at these ponds, Zone 3 species may not be present every year due to high water levels.

Zone 4 – Low herbacous and emergent species on semi-permanently flooded organic-rich pond bottom sediments. Common species include *Eleocharis ovata*, *E. flavescens*, *E. palustris*, *Scirpus smithii*, *S. pungens*, *Dulichium arundinaceum*, *Juncus pelocarpus*, *Sagittaria graminea* var. *graminea*, *Eriocaulon aquaticum*, *Ludwigia palustris*, *Gratiola aurea*, *Lindernia dubia* var. *dubia*, and *Utricularia gibba*. Emergent species with floating leaves found stranded on the exposed bottom include *Nuphar variegata*, *Nymphaea odorata*, *Brasenia schreberi*, *Potamogeton epihydrus*, and *P. bicupulatus*. Organic sediment accumulations in exposed pond bottom areas may be quite deep depending on basin morphometry. At Gamache Pond, Ludlow, a soil pit revealed 3.5 vertical feet of muck overlying basal mineral sediment in one portion of the pond interior. During the fall of 2002 after extended severe drought, dessicating organic sediments on the exposed bottom of Gamache Pond were deeply fissured to the basal mineral horizon in many areas.

Zone 5 – Emergent and aquatic species in permanently flooded portions of the pond. Common emergent or floating species in Zone 5 include *Nuphar variegata*, *Nymphaea odorata*, *Brasenia schreberi*, *Potamogeton epihydrus*, *P. bicupulatus*, and *Utricularia vulgaris*. Emergent species with floating leaves (particularly *N. odorata*) may locally cover much of the pond surface.

FLORISTICS AND RARE SPECIES

Sandy exposed pondshores at sites in the Lower Connecticut River Valley support a suite of distinctive plant species similar to those that occur on sandy pondshores on the coastal plain of southern New England and further south. These disjunct distributions may be the result of recent chance northward dispersal of propagules by migrant bird species, or may represent remnants of a relict southern flora that

extended northward into New England via the Connecticut River Valley during the postglacial hypsithermal period (see Zebryk 1991). The species are as follows: *Sagittaria teres*, *Rhynchospora scirpoides*, *R. macrostachya*, *Carex longii*, *Panicum verrucosum*, *Xyris difformis* var. *difformis*, *Fimbristylis autumnalis*, *Hemicarpha micrantha*, *Fuirena pumila*, *Juncus pelocarpus*, *Eriocaulon aquaticum*, *Scleria reticularis* (historic occurrence at Mona Lake, Springfield; Andrews 1924), *Rotala ramosior*, *Rhexia virginica*, *Hypericum mutilum*, *Gratiola aurea*, and *Viola lanceolata*. Several of these species (i.e., *Sagittaria teres*, *Rhynchospora scirpoides*, *Fuirena pumila*, *Scleria reticularis*, and *Rotala ramosior*) are quite rare in the Commonwealth, particularly so in western Massachusetts where they are disjunct (Sorrie and Somers 1999), and seem to be specific to the sandy pondshore community type. Although not considered uncommon in this habitat type in the coastal counties of Massachusetts, *P. verrucosum* is also disjunct at a few sandy pondshores in western Massachusetts. Andrews (1924) recorded the occurrence of the coastal plain species, *Orontium aquaticum* in a "pool" approximately one mile southwest of Mona Lake; however, this species was not observed at any of the sites in 2002.

Although bearing floristic similarities to coastal plain pondshores in Massachusetts, inland pondshores in western Massachusetts appear to have significant differences in terms of composition. This can be expressed primarily by the absence of a large number of species (mostly rare) that are described as being characteristic of, or specific to, pondshores in the coastal counties and on Long Island. For comparison see Swain and Kearsley (2000) and Zaremba and Lamont (1993).

During the course of the 2002 field surveys, a significantly large, previously unknown population of the state-endangered species *Rotala ramosior* was discovered in a cove at the northeast corner of Minechoag Pond, Ludlow. Occurring both on exposed sands and organic pond bottom sediments (i.e., Zones 3 and 4), many thousands of flowering and fruiting *Rotala* individuals were observed in association with typical Zone 3 and 4 species. This population was much larger both in terms of area and number of individuals compared to the population at Ashley Reservoir, Holyoke, which formerly was the only known occurrence of *Rotala* in similar habitat in western Massachusetts (Zebryk 1998). Also present at Minechoag Pond was a large population of *Ludwigia polycarpa* comprising tens of thousands of individuals distributed over most of the shoreline in Zones 2 and 3. Primarily a midwestern species, *L. polycarpa* is at its eastern range limit in western New England, and is considered threatened in Massachusetts. Other species of interest found at Minechoag

Pond include *Panicum philadelphicum*, *P. verrucosum*, *Xyris difformis* var. *difformis*, *Eriocaulon aquaticum*, *Polygonum careyi*, and *Proserpinaca palustris*.

A remarkably large population of *Rhynchospora scirpoides* consisting of thousands of individuals was observed in Zones 3 and 4 at Gamache Pond, Ludlow, where it occurred among a dense, lawn-like assemblage of graminoid and herbaceous species. Notable associates included *R. macrostachya*, *R. capitellata*, *R. alba*, *Fuirena pumila*, *Panicum philadelphicum*, *Xyris difformis* var. *difformis*, *Eriocaulon aquaticum*, and *Drosera intermedia*. During the early fall of 2002, Gamache Pond was the only site visited that had drawn down to the extent that no ponded water was present in the basin. It is suspected that the hydrological regime at this site has changed over the years, as there has been considerable woody plant encroachment (*Decodon verticillatus*, *Cephalanthus occidentalis*) into many portions of the basin interior.

Collections of *Carex longii* (Lake Lorraine, *T.M. Zebryk 7839*, MICH) and *Gnaphalium purpureum* var. *purpureum* (Five Mile Pond, *T.M. Zebryk 7784*, MICH) are apparent Hampden County records, and represent disjunct populations of species previously known only from coastal counties in Massachusetts (Sorrie and Somers 1999; Ray Angelo, NEBC, pers. comm.). *Gnaphalium* is exceedingly rare throughout New England (Brumback and Mehrhoff et al. 1996).

Callistephus chinensis, a showy annual member of the Asteraceae native to East Asia, was documented for the the first time in Massachusetts at Bass Pond, Springfield (*T.M. Zebryk 7981*, NEBC). Growing without cultivation and evidently originating from seed, a single depauperate plant was observed with other low native and introduced annual herbaceous species on a portion of sandy exposed pondshore. This taxon has been recorded only once before in New England, at Mount Desert Island, Maine (Ray Angelo, NEBC).

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APPENDIX

FLORISTIC COMPARISON, INLAND SANDY ACID PONDSHORES, HAMPDEN COUNTY, MASSACHUSETTS

Site name abbreviations: Five Mile Pond (FIVE); Lake Lorraine (LORR); Mona Lake (MONA); Loon Pond (LOON); Bass Pond (BASS); Dimmock Pond (DIMM); Long Pond (LONG); Spectacle Pond (SPEC); Longmeadow Pond (LOME); Minechoag Pond (MINE); Gamache Pond (GAMA); Haviland Pond (HAVI); Murphy Pond (MURP). HIST – historic occurrence. Voucher specimens on deposit at NEBC, MICH, EIU; the author's collection numbers are in italics.

LILIOPSIDA (Monocots)

ALISMATACEAE. *Sagittaria engelmanniana* – FIVE, LORR, MONA, DIMM, SPEC, LOME, MINE, GAMA, MURP; *7801, 7939*. *Sagittaria graminea* var.

graminea – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, MINE, GAMA, MURP; *7799, 7912. Sagittaria teres* – FIVE, LORR, SPEC; *7800, 7841.*

CYPERACEAE. *Carex longii*—LORR; *7839. Cyperus bipartitus* – FIVE, LORR, MONA, LOON, DIMM, LONG, SPEC, MINE, GAMA, HAVI, MURP; *7768, 7843. Cyperus dentatus* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7790, 7804, 7821, 7852. Cyperus diandrus* – FIVE, MONA, DIMM, MINE, GAMA; *7786, 7950. Cyperus erythrorhizos* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7769, 7908, 7937. Cyperus squarrosus* – FIVE, LORR, MONA, LOON, DIMM, SPEC, MINE, GAME, HAVI; *7897. Cyperus strigosus* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7819, 7865, 7941. Dulichium arundinaceum* – FIVE, MONA, LOON, DIMM, LONG, SPEC, MINE, GAMA, MURP; *7850, 7956. Eleocharis acicularis* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7781. Eleocharis flavescens* – FIVE, LORR, MONA, LOON, DIMM, LONG, SPEC, MINE, GAMA, HAVI, MURP; *7785, 7816. Eleocharis ovata* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7924, 7931, 7940. Eleocharis palustris* – FIVE, LORR, MONA, LOON, DIMM, LONG, SPEC, MINE, GAMA, HAVI, MURP; *7914. Fimbristylis autumnalis* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7772, 7818, 7906. Fuirena pumila* – FIVE, MONA, SPEC, MINE, GAMA; *7823, 7863, 7902. Hemicarpha micrantha* – FIVE, LORR, MONA, LOON, SPEC, MINE, GAMA, HAVI; *7788, 7842; 7895. Rhynchospora alba* – GAMA; *7959. Rhynchospora capitellata* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7771, 7846, 7898. Rhynchospora macrostachya* – SPEC, GAMA; *7862; 7957. Rhynchospora scirpoides* – MONA (HIST), GAMA; *7943. Scirpus cyperinus* – MONA, LOON, DIMM, LONG, SPEC, MINE, GAMA, MURP. *Scirpus pungens* – FIVE, LORR, MONA, LOON, DIMM, SPEC, GAMA, HAVI, MURP. *Scirpus smithii* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7809, 7905, 7933, 7948. Scirpus validus* – SPEC; *7859. Scleria reticularis* – MONA (HIST).

ERIOCAULACEAE. *Eriocaulon aquaticum* – FIVE, LORR, MONA, LOON, LONG, SPEC, MINE, GAMA, HAVI; *7778, 7899.*

JUNCACEAE. *Juncus acuminatus* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP. *Juncus brevicaudatus* – FIVE, LORR, MONA, DIMM, LONG, SPEC, LOME, MINE, GAMA; *7767, 7952. Juncus canadensis* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7811, 7953. Juncus marginatus* – FIVE, LORR, LOON, LONG, SPEC, MINE, GAMA. *Juncus pelocarpus* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7793, 7860, 7904. Juncus tenuis* – FIVE, LORR, LOON, BASS, DIMM, LONG, SPEC, MINE, HAVI; *7766, 7783.*

POACEAE. *Digitaria filiformis* – FIVE, MONA, LOME, MINE; *7829, 7916. Echinochloa muricata* var. *muricata* – FIVE, LORR, MONA, LOON, BASS,

DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7854. Eleusine indica* – FIVE, LORR, HAVI; *7795. Leersia oryzoides* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7949. Panicum dichotomiflorum* FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7808, 7810, 7893. Panicum lanuginosum* var. *fasciculatum* LORR, MONA, LOME, MINE; *7807, 7838. Panicum meridionale* – DIMM; *7851. Panicum philadelphicum* – FIVE, LORR, MONA, DIMM, SPEC, LOME, MINE, GAMA; *7820, 7822, 7911, 7960. Panicum rigidulum* – FIVE, LORR, MONA, LOON, DIMM, LONG, SPEC, LOME, MINE, GAMA. *Panicum verrucosum* MONA, DIMM (HIST), MINE; *7871, 7903. Poa palustris* – LONG, GAMA; *7773, 7802.*

POTAMOGETONACEAE. *Potamogeton bicupulatus* – FIVE, LORR, MONA, LOON, DIMM, LONG, SPEC, MINE, HAVI, MURP; *7776. Potamogeton epihydrus* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP.

SPARGANIACEAE. *Sparganium americanum* – SPEC, MONA, LONG, MINE, GAMA, MURP; *7858.*

XYRIDACEAE. *Xyris difformis* var. *difformis* FIVE, LOME, MINE, GAMA; *7896, 7934.*

MAGNOLIOPSIDA (Dicots)

ACERACEAE. *Acer rubrum* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP.

ASTERACEAE. *Bidens cernua* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7917, 7951. Bidens connata* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7954. Callistephus chinensis* BASS; *7981. Erechtites hieraciifolia* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7923. Eupatorium perfoliatum* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7855. Gnaphalium obtusifolium* BASS; *7982. Gnaphalium purpureum* var. *purpureum* – FIVE; *7784. Gnaphalium uliginosum* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7794, 7915.*

BETULACEAE. *Alnus serrulata* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP.

BRASSICACEAE. *Cardamine pensylvanica* – LONG; *7760. Rorippa palustris* var. *fernaldiana* – LONG; *7763.*

CABOMBACEAE. *Brasenia schreberi* – FIVE, LORR, MONA, LOON, DIMM, LONG, SPEC, MINE, HAVI, MURP.

CLETHRACEAE. *Clethra alnifolia* – FIVE, LOON, DIMM, LONG, LOME, MINE, GAMA.

CLUSIACEAE. *Hypericum canadense* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7787*, *7789*, *7817*, *7909*. *Hypericum mutilum* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7946*. *Triadenum fraseri* – LONG; *7759*. *Triadenum virginicum* – FIVE, MONA, DIMM, LONG, MINE, GAMA, MURP; *7847*.

DROSERACEAE. *Drosera intermedia* – GAMA; *7935*.

ERICACEAE. *Lyonia ligustrina* – FIVE, LORR, LOON, DIMM, LONG, SPEC, LOME, MINE, GAMA. *Vaccinium corymbosum* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP.

EUPHORBIACEAE. *Euphorbia maculata* – FIVE, LORR, LOON, BASS, DIMM, LONG, HAVI; *7827*.

HALORAGACEAE. *Myriophyllum humile* – FIVE, LORR, DIMM, MINE, GAMA, MURP; *7894*. *Proserpinaca palustris* – MINE, GAMA; *7901*, *7958*.

LAMIACEAE. *Lycopus americanus* – MINE; *7928*. *Lycopus uniflorus* – FIVE, LORR, MONA, LOON, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP. *Mentha arvensis* – LONG, MINE; *7918*.

LENTIBULARIACEAE. *Utricularia gibba* – FIVE, LORR, MONA, LOON, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7765*, *7932*. *Utricularia purpurea* – MINE; *7926*. *Utricularia resupinata* – MONA (HIST). *Utricularia vulgaris* – FIVE, LORR, MONA, LONG, SPEC, MINE, HAVI, MURP.

LYTHRACEAE. *Decodon verticillatus* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7955*. *Lythrum salicaria* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7826*. *Rotala ramosior* – MINE; *7922*.

MELASTOMATACEAE. *Rhexia virginica* – FIVE, LOME, GAMA; *7849*.

MYRICACEAE. *Myrica gale* - FIVE, LORR, LOON, DIMM, LONG, LOME, MINE, GAMA, HAVI, MURP.

NYMPHAEACEAE. *Nuphar variegata* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, MINE, GAMA, HAVI, MURP; *7947*. *Nymphaea odorata* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, MINE, GAMA, HAVI, MURP.

NYSSACEAE. *Nyssa sylvatica* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7857*.

ONAGRACEAE. *Epilobium ciliatum* var. *ciliatum* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7792. Ludwigia alternifolia* – FIVE, LORR, MONA, LOON, DIMM, SPEC, MINE, GAMA, MURP; *7840. Ludwigia palustris* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7927. Ludwigia polycarpa* – MINE; *7929.*

POLYGONACEAE. *Polygonum amphibium* var. *emersum* – FIVE, LONG, MINE, GAMA, HAVI, MURP; *7919. Polygonum careyi* – FIVE, MONA, DIMM, MINE, GAMA, MURP; *7825, 7868. Polygonum hydropiper* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7774, 7797, 7925. Polygonum hydropiperoides* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7815, 7824. Polygonum lapathifolium* – MONA, LONG, MINE, GAMA, MURP; *7775, 7805. Polygonum pensylvanicum* MONA, MINE, GAMA, MURP; *7866, 7942. Polygonum punctatum* var. *punctatum* FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7798, 7869. Polygonum sagittatum* – FIVE, LORR, MONA, DIMM, LONG, SPEC, LOME, MINE, GAMA, MURP; *7867. Rumex orbiculatus* – FIVE; *7803.*

RANUNCULACEAE. *Ranunculus pensylvanicus* – SPEC, MURP; *7861, 7930.*

RHAMNACEAE. *Rhamnus frangula* – MONA, LOON, DIMM, LONG, LOME, MINE, GAMA, HAVI, MURP.

ROSACEAE. *Potentilla norvegica* – FIVE, MINE, MURP; *7921.*

RUBIACEAE. *Cephalanthus occidentalis* – FIVE, LORR, MONA, DIMM, LONG, SPEC, MINE, GAMA, MURP.

SALICACEAE. *Salix nigra* – MONA; *7864.*

SCROPHULARIACEAE. *Agalinis purpurea* var. *purpurea* - FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7770, 7779, 7784, 7814. Gratiola aurea* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7845. Lindernia dubia* var. *anagallidea* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7782, 7813, 7938. Lindernia dubia* var. *dubia* – FIVE, LORR, MONA, LOON, BASS, DIMM, LONG, SPEC, LOME, MINE, GAMA, HAVI, MURP; *7945.*

VERBENACEAE. *Verbena hastata* – FIVE, LORR, MONA, BASS, DIMM, LONG, MINE, GAMA, HAVI, MURP; *7780.*

VIOLACEAE. *Viola lanceolata* var. *lanceolata* – FIVE, DIMM, LOME, MINE, GAMA, MURP; *7791, 7853.*

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IN MEMORIAM

Craig William Greene
1949–2003

Craig William Greene, the Elizabeth Battles Newlin Chair in Botany at the College of the Atlantic (COA) in Bar Harbor, Maine, died on 2 October 2003 following a long struggle with pancreatic cancer. He is missed by family, friends, students, and colleagues for his enthusiasm, professional accomplishments, and friendship.

Craig was born in Geneva, New York and earned a B.S. from SUNY College of Environmental Science and Forestry, Syracuse, majoring in Forest Botany. He received an M.Sc. in Plant Taxonomy from the University of Alberta, where he worked on the taxonomy of *Smelowskia calycina* (Cruciferae) in North America under the guidance of John G. Packer. His Ph.D. was in Biology from Harvard University, his major advisor was Reed C. Rollins, and his dissertation was "The Systematics of *Calamagrostis* (Gramineae) in eastern North America."

After completing his Ph.D. in 1980, Craig went to COA where he was a revered teacher and active in many other parts of the institution. Craig's teaching gift came from his broad understanding of the natural world, clarity of expression, and compassion for students. In Alberta, in Cambridge, and at COA, he taught a wide range of courses. In more

than two decades at COA, he offered courses in Biology, Economic Botany, Introductory Botany, Genetics, Morphology and Diversity of Plants, Natural History, Plant Taxonomy, Plant Systematics, Population and Community Ecology, and Woody Plants. He especially enjoyed field courses and took students to many wonderful sites on Mount Desert Island (MDI). He chaired several committees at COA and, starting in 1996 was Associate Dean of Advanced Studies with administrative responsibility for the Masters of Philosophy in Human Ecology.

Craig's research focused on agamic complexes and the coastal flora of Maine. His work on high polyploidy, facultative agamospermy, and complex patterns of morphology in *Calamagrostis* (Poaceae) was a significant contribution to our knowledge of evolution in agamic complexes. His interest in *Calamagrostis* also included floristic treatments, such as *The Jepson Manual* (California), *Vascular Plants of British Columbia*, and *Flora of North America* (his treatment is in press). Craig's expertise in agamic complexes easily translated to *Amelanchier* (Rosaceae), which was particularly attractive because coastal Maine is a center of diversity of the genus. Craig got COA students involved in getting chromosome counts, carrying out experimental pollinations, and assessing patterns of population variability in populations of MDI shadbushes. Craig held high standards in his research and publications. His science was founded on rigorous methodology and lead to prudent conclusions that were succinctly presented and illustrated with high-quality graphics.

Not long after moving to Maine, Craig began working on its coastal flora, especially on MDI and in Acadia National Park. With students and collaborators, he carried out surveys of endangered plant species and freshwater aquatic vegetation. He worked for many years on the flora of the park, and a publication on this flora is in preparation. He was an ecological consultant for Acadia National Park starting in 1985 and a member of the Maine Endangered Plant Technical Advisory Committee (later called the Botanical Advisory Group) starting in 1987.

Craig balanced his commitment to his profession with devotion to family and friends. He also sustained passionate interests in fly-fishing, home-brewing, bicycling, and nature photography. He had a life-long love of fishing mountain brooks, especially those near the Adirondack cabin built by his great grandfather and grandfather in 1911. Many friends delighted in his high-quality home brews, which were also home-labeled with names such as Otter Ale and Badger Beer. His beer-brewing log records a total of 1535 gallons, with production extending

into the last year of his life. In the late 1980s Craig took up bicycling. He helped organize and rode in the annual Tour de Cure fund-raising ride on MDI every year that it was held, including 2003. Except for that year, he always rode the 100-kilometer option in the tour, a beautiful ride near the shores of MDI. During his many botanical field trips, Craig took pictures. In the past couple of years he developed some of his favorites, and they reflect his love of the natural world and his creativity. There was a show of his photographs at COA in 2002.

The high esteem held for Craig was clearly evident on 21 May 2003 when the Botany Lab at COA was dedicated to him. The event packed an auditorium with COA faculty and staff, current and former students, and family, as well as many professional colleagues and friends from near and far. For almost three hours, there was heart-felt gratitude, fond recollections, and praise for all Craig did for so many people. The words on the bronze plaque outside the Botany Lab summarize his stature: "His knowledge, excellence in teaching, and enthusiasm for the role of plants in human affairs have inspired two decades of students and beautified the landscape of our campus."

Craig was supported throughout his illness by family and many friends, and he died at home among them.

—Christopher S. Campbell, Department of Biological Sciences, University of Maine, Orono, ME 04469-5722.

RHODORA, Vol. 106, No. 925, pp. 80–83, 2004

BOOK REVIEW

The Herbaceous Layer in Forests of Eastern North America by F. S. Gilliam and M. R. Roberts, eds. 2003. xvi + 408 pp. illus. ISBN 0-19-514088-5 $85.00 (hardcover). Oxford University Press, New York.

This volume, developed in a conversation that included several technical symposia over three years, is distinctive in treating the herbaceous layer of forests as the focus of attention, and like all such volumes, provides a useful review of a wide swath of research. It is not surprising that a comprehensive survey of the known points out some of the things unknown and requiring further research, and in fact an interesting feature of this volume is that the editors take the time in the final chapter not only to summarize what they consider to be findings well established in the preceding chapters, but also to list specific areas they consider important for future research.

Chapter 1 suggests a conceptual framework for thinking about the forest herbaceous layer, based on a distinction between resident species, that is, species whose height is always less than 1–1.5 m ("or perhaps others," say Gilliam and Roberts), and transient species, that is, species that are only temporary elements of this zone, because they will emerge into the mid- or upper stories of the forest. Thus, the former group includes the "herbs proper" plus some low shrubs, while the latter group includes seedlings of trees and shrubs (and vines, not mentioned much in this book). This distinction is intuitive with respect to many questions that bear on community assemblage and change, such as reproduction/dispersal, nutrient use and foraging, or resilience when faced with various kinds of disturbance. However, the conceptual framework disappears for vast stretches of this book, only to appear to best effect in discussions of mechanisms linking different strata in the forest (Section 4).

Section 1 provides some background information on the ecology and ecophysiology of herbaceous plants, and it is perhaps worth noting that a significant proportion of the literature cited is not in fact drawn from research on forests of eastern North America alone. This is not a liability, really, but it does point to gaps in our knowledge of the area treated. Chapter 2, "Nutrient relations of the herbaceous layer in deciduous forest ecosystems" (Muller), gives a valuable summary of what is known about the role of herbaceous species in nutrient flow in forested systems. The author considers and revisits the notion of the vernal dam—the idea that spring ephemerals, active before the overstory, and

during the first mobilization of nutrients, sequester key nutrients which are later released to the soil, and thus made accessible to later-appearing species rather than being lost. While Muller rehashes some evidence suggestive of this, he also reports evidence that a "vernal dam" may be in operation, but that it is composed of the microbial fauna rather than the herbs. Beyond this, he presents evidence that in some cases, at least, the spring ephemerals' sequestration of nutrients may actually speed their departure from the system, and thus impoverish rather than enrich the environment for later-appearing species. The other two chapters in the section are Neufeld and Young's "Ecophysiology of the herbaceous layer in temperate deciduous forests," which generally focuses on light relations and physiology, and Anderson's "Interactions of nutrient effects with other biotic factors in the herbaceous layer." This latter, while interesting, proves rather cursory when it describes the nutrient aspects of herbivory and mycorrhizal associations. This may reflect the state of the science in this area; still, it is surprising that in this as in other chapters, no real attention is paid to recent work on below-ground interactions between plants, and plants and herbivores [see, for example, references and findings discussed in Bardgett and Wardle (2003) and Van der Putten (2003)].

Section 2: "Population dynamics of the herbaceous layer" is a monotypic section, comprising the single article "Populations of and threats to rare plants of the herb layer: More challenges and opportunities for conservation biologists" (Jollis). This chapter is an overview of key conceptual and analytic ideas in conservation biology, of particular use to readers not familiar with the field. Jollis keys her discussion to two useful charts, in which 94 endangered or threatened species are characterized by status and range, and interestingly by life-history characteristics (e.g., breeding systems, dispersal mechanisms). [I think "range" means "range within which the species is threatened," the only way I can make sense of the endangered status of *Chimaphila maculata*, range given as "Canada, esp. Ontario." See for example Brumback and Mehrhoff, et al. (1996), where *C. maculata* does not appear.] The clearest conclusion of the author is that for herbaceous species of the region, and especially the rare or endangered species, our ignorance of population biology is discouragingly large.

Section 3 addresses "Community Dynamics of the herbaceous layer across spatial and temporal scales," and includes chapters on "The herbaceous layer of eastern old-growth deciduous forests" (McCarthy); "Habitat heterogeneity and maintenance of species in understory communities" (Beatty); "Interaction between the herbaceous layer and

overstory canopy of Eastern forests: A mechanism for linkage" (Gilliam and Roberts); "Temporal and spatial patterns of herbaceous layer communities in the North Carolina Piedmont" (Christenson and Gilliam); and "Composition and dynamics of the understory vegetation in the boreal forest of Quebec" (Grandpré et al). In this section, I highly recommend Beatty's chapter describing her 20 years of research on the population and metapopulation dynamics of species in response to micro-site alterations such as pit and mound formation over time. While (of course) more research remains to be done, her findings go far to explain both the positive and negative contributions of habitat heterogeneity in maintaining species in the landscape.

Section 4 addresses "Community dynamics of the herbaceous layer and the role of disturbance," and here the conceptual point raised by the editors in Chapter 1 finally comes into play, as the heterogeneous composition of the "herbaceous" layer (including both residents and transients) plays out with respect to succession, regeneration after disturbance, and invasibility. The chapters of this section are: "The herbaceous layer as a filter determining spatial pattern in forest tree regeneration" (George and Bazzaz); "Invasion of forests in the eastern United States" (Luken); and "Response of the herbaceous layer to disturbance in eastern forests" (Roberts and Gilliam). The latter two papers are strictly reviews, while George and Bazzaz's paper provides both an overview of the literature and a discussion of data generated in their research on the question of "filtering," especially by herbaceous species that form a "canopy" of their own (e.g., *Dennstaedtia punctilobula*). Luken's paper on the characteristics of invaders and invasibility leaves the reader with the feeling that, while more research is required on these interesting and important areas, perhaps the "summative" questions asked up until now (e.g., What are the characteristics of an invasive plant? What are the characteristics of an invasible forest?) are not the most productive ones, given the tremendous variety of "invasives," and the great complexity of site types with which they interact.

Gilliam and Roberts return for a Synthesis section: "The dynamic nature of the herbaceous layer: Synthesis and future directions for research." This provides a lucid and welcome overview of the major findings reported in the previous chapters in a way that provides some theoretical coherence, and concludes with suggestions for future research emerging from the papers in each of the 4 topical sections. While the book does not provide systematic or even coverage of its title subject, it does represent a useful contribution to the study of a complex and rapidly changing region which we tend (mistakenly) to think of as well known.

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BARDGETT, R. D. AND D. A. WARDLE. 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84: 2258–2268.

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VAN DER PUTTEN, W. H. 2003. Plant defense belowground and spatiotemporal processes in natural vegetation. Ecology 84: 2269–2280.

—BRIAN DRAYTON, TERC, 2067 Massachusetts Ave., Cambridge, MA 02140.

RHODORA, Vol. 106, No. 925, pp. 84, 2004

NEW BOOKS

Flora of the Hudson Bay Lowland and its Postglacial Origins by J. L. Riley. 2003. viii + 236 pp. 32 color plates, distribution maps. ISBN 0-660-18941-0 US$49.95 (softcover). NRC Research Press, National Research Council of Canada Building M-55, Ottawa, Ontario K1A 0R6, Canada.

Genera Orchidacearum, Volume 3: Orchidoideae (Part Two), Vanilloideae by A. M. Pridgeon, P. J. Cribb, M. W. Chase, and F. N. Rasmussen, eds. 2003. xviii + 360 pp. 105 color plates, line drawings, distribution maps. ISBN 0-19-850711-9 $150.00 (hardcover). Oxford University Press, New York.

Inferring Phylogenies by J. Felsenstein. 2004. xx + 664 pp. illus. ISBN 0-87893-177-5 $59.95 (softcover). Sinauer Associates, Inc., Sunderland, MA.

Medical Botany: Plants Affecting Human Health, Second Edition by W. H. Lewis and M. P. F. Elvin-Lewis. 2003. 832 pp. ISBN 0-471-62882-4 $95.00 (hardcover). John Wiley & Sons, Inc., Hoboken, NJ.

The Palm Book of Trinidad and Tobago, Including the Lesser Antilles by P. L. Comeau, Y. S. Comeau, and W. Johnson. 2003. xi + 108 pp. color photos, line drawings, distribution maps. ISBN 0-9740870-0-9 US$39.95 (softcover). Published by the International Palm Society. [order on line at: www.palms.org]

Plant Genomics and Proteomics by C. A. Cullis. 2004. xiv + 214 pp. illus. ISBN 0-471-37314-1 $69.95 (hardcover). John Wiley & Sons, Inc., Hoboken, NJ.

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NEBC MEETING NEWS

October 2003. Vice President Art Gilman introduced the night's speaker, Bill Patterson, from the University of Massachusetts, Amherst. Bill, who has been interested in fire ecology since his undergraduate years, is currently a National Park Service certified "Burn Boss," and also instructs The Nature Conservancy in burning techniques.

Bill noted that for over 60 years, Americans have been trained to follow the mantra of Smokey the Bear: forest fires are bad. Providing land managers and the public with the historical background of an ecosystem aids in convincing them to trust in the ability of fire to maintain that ecosystem. Historical records indicate that Native Americans practiced regular burning of the landscape. However, some people now believe that there has been some exaggeration as to how frequent and widespread the burning was. To investigate this, Bill and his team laid a series of 20 m^2 plots at the Cape Cod National Seashore (CCNS). These plots, monitored over the past 18 years, were subjected to combinations of the following treatments: burning/mowing during each growing season, at 1–4 year intervals, or leaving plots unburned. After 2–3 years, the plots that were burned annually had so little fuel remaining, it was difficult to even start fires in them. New species were not recruited with this burning regime, and the plots did not convert to grassland, indicating that although Native Americans may have burned land annually, they could not have been burning the same tracts of woodlands as frequently as has been assumed.

Determining an ecosystem's "fire history" can be difficult in New England, since there are so few older trees that scientists can examine for scarring patterns in order to estimate when fires occurred. One technique that has been successful is the examination of the sediment of pond cores. Using pollen grains and charcoal present in these cores, scientists have been able to determine the composition of ancient forests as well as the occurrence of fires.

To determine how best to manage the Atlantic white cedar swamp at Marconi Station on the CCNS, the only major population of this species on Park Service land in 1980, a core of the swamp peat was taken. The Park Service was concerned that with total fire suppression, the cedar was in danger of being replaced by red maple. The 1000-year-long core revealed that the cedar had become abundant only over the past 350 years, possibly due to the occurrence of a major fire. Prior to the fire, the population had fluctuated continuously in response to periodic fires, which probably originated in the upland. The amount of charcoal in the core indicated that these fires were large, and therefore too risky to

reproduce. Since the cedar continues to thrive without fire, it was decided that there was no need to harvest or burn the stand in the immediate future.

There are a variety of techniques now used to develop and implement a burn plan. Past fire occurrences are investigated with satellite photography, and burn crews frequently have helicopters to assist them. Crews sometimes use chemical-filled "ping pong balls" to start mini-fires before the main burn; sending in the ping pong balls ahead of time ensures that there are burned-out areas inside the targeted plot, which keeps the fire from spreading out of control. For safety reasons, Bill and other burn bosses have had to work closely with fire departments, and for most burns there is backup equipment present in case of emergency. The Air Quality Division of the Department of Environmental Protection monitors smoke production, further constraining the burning that can be done. Bill noted that he has never had a fire escape from the control of one of his crews, but is well aware of the nuisance that occurred when a seven-acre fire planned in Albany, New York a few years ago instead burned through 75 acres of land.

Bill shared some of the valuable experience he has acquired in his twenty years of practicing fire ecology. For many years, it was standard to burn only in the spring, and Massachusetts granted permits only for that time of the year. While working on Nantucket in 1983, his crew was granted a permit to burn in August, for a project to prevent shrub succession in sandplain grasslands. He has since learned that the best way to control many hardwood species is to cut or burn them in midsummer. At that time of year the fires are intense, but don't spread as fast as those set in the spring, reducing the chance of the fire escaping from the control of the burn crew. Bill ended his talk by recommending that land managers seeking to control shrubs and trees should employ a burning regime during the growing season; if land is burned during the dormant season, the treatment will have to be repeated annually just to maintain the status quo.

November 2003. Vice President Art Gilman introduced the night's speaker, Dave Houston. Dave, now retired, was a Principal Plant Pathologist at the Center for Forest Health Research, part of the U.S.D.A. Forest Service's Northeastern Forest Experiment Station. The title of his talk was "Beech-bark disease and its effects on the northern forest." His research on beech bark disease spans three decades, beginning in the 1960s.

Dave began by describing several interesting characteristics of beech trees (*Fagus* spp.). They have amazing longevity (400+ years), reproduce both sexually (they are prolific seeders) and asexually (by

root suckers), and can tolerate deep shade, allowing them to grow for years in the forest understory until a gap in the canopy allows them to thrive. Beech trees also have atypical bark, with only a thin layer of dead cells surrounding the inner living bark and cambium. This lack of a protective rhytidome barrier makes the bark of beech trees more susceptible to mechanical, fire, or insect damage.

Beech bark disease (BBD) is caused by a combination of two organisms: the beech scale insect (*Cryptococcus fagisuga*), and fungi from the genus *Nectria* (principally *N. galligena* and *N. coccinea* var. *faginata*). The first North American appearance of the beech scale insect was around 1890 in Nova Scotia, where it was introduced via imports of European beech trees. Over the next several decades the scale spread north, then west and south; multiple introductions are suspected. They can now be found throughout the northeastern United States, west to Michigan, and south as far as North Carolina. The scale insects are tiny, and are all female, reproducing parthenogenetically. The nymphs are mobile, seeking out bark fissures and callus tissue from which they can feed, using a long, probing stylet. Once established, the scale insects can increase rapidly, secreting a waxy "wool" that can cover the outside of the tree when conditions are favorable.

Injury to beech bark by scale insects is a necessary precedent to infection by *Nectria* fungi. While *N. galligena* is native, and may be present in a forest before the scale insects invade, *N. coccinea* var. *faginata* was introduced, and always follows the scale into a new habitat. Reproduction is both asexual and sexual. Red perithecia, the sexual fruiting bodies, produce ascospores, the primary infective propagules. Dave noted that scale infestation and subsequent fungal infection is often most abundant on the north-facing side of a tree.

The initial wave of the disease, where up to 80% of large, mature beech can be killed, is termed the "killing front." Following this is an "aftermath stage," in which the disease affects young trees of root sprout and seedling origin. Such trees are not killed quickly, as were their progenitors, and accumulate cankers and defects over time. In a study done to quantify the damage to beech trees in aftermath forests, a regional pattern of canker development was found. The pattern was correlated with cold winters and wet falls, which served to reduce scale populations. Diseased trees often exhibit bizarre bark patterns as cankers develop, and in turn, become refuges for further infestation and infection. After the talk concluded, curious attendees were able to view samples of infected trees.

Researchers are now focused on the potential exploitation of BBD-resistant beech. In one case, trees initially thought to be resistant were

actually being protected by crustose lichens that encased the trunk and prevented scale insects from feeding. During the search for resistant phenotypes, Dave uncovered a curious phenomenon: semicircles of trees that were all BBD-resistant. Though it was suspected that these trees were clones produced by root suckering, isozyme analysis showed that the trees were unique, that is, were derived from seed and probably shared a single parent. It turned out that the agents responsible for this pattern were blue jays. A blue jay, which can tuck up to 14 seeds from a single beech tree in its throat, will cache the seeds in a semicircle. Seeds that are not recovered may become founding populations, and if they produce root sprouts, larger groups of resistant trees can result.

While Dave was hoping to spend the greater part of his retirement "shepherding resistant genotypes into the forest," the work to develop BBD-resistant beech trees has been difficult. Researchers have been unable to easily propagate beech vegetatively (beech can be vegetatively propagated, but only with difficulty), and it is difficult to conduct control pollinations between desired genotypes. Dave concluded his talk by noting that the rising demand by foresters and arboreta for resistant trees will spur research over the next few years, and will hopefully yield successful results.

December 2003. Vice President Art Gilman introduced Arthur Haines as the night's speaker. Arthur is a plant biologist and field taxonomist working as a researcher at the New England Wild Flower Society (NEWFS). He spoke to the club about his current work for NEWFS: "The Herbarium Recovery Project: Surveying herbaria for species of regional conservation concern."

Arthur began by describing the project, a reevaluation of herbarium specimens of rare species and the creation of an electronic database of herbarium records. The study included examination of collections from 42 New England herbaria. Arthur noted the value of herbaria in providing botanists with voucher specimens that can be used for their distribution data as well as for morphological and genetic studies.

Records for more than 500 native tracheophytes were reevaluated and recorded for this massive study, in which species at all levels of conservation value were treated. Many of these species are categorized as Division 1 in the *Flora Conservanda*, indicating that they have fewer than 100 global occurrences. Examples include the Anticosti aster (*Symphyotrichum anticostensis*), found in New England only within the Aroostook River in northern Maine, and the globally rare northeastern bulrush (*Scirpus ancistrochaetus*). Examples of Division 2 species (fewer than 20

New England occurrences) included in the study are pale painted-cup (*Castilleja septentrionalis*) and Greene's violet (*Viola subsinuata*), native to western New England. Selected species from Divison 4, which have no extant New England occurrences (i.e., known only from historical records), included disjunct eyebright (*Euphrasia disjuncta*), the only herbarium record of which was lost in a fire. There were also species for which data were lacking, labeled as "Division Indeterminate." Examples include newly described species such as MacGregor's wild rye (*Elymus macgregorii*), as well as Wiegand's rush (*Juncus anthelatus*), which was recently given species status. Arthur induced hearty laughter from the crowd when he displayed a photo of one of the most peculiar specimens he came across: a cookie with an imprint of *Isotria medeoloides*, a Division 1 species. It was later explained by an audience member that the cookies were served at a student's thesis defense.

All data from the herbarium specimens, including annotations, have been recorded in a Microsoft Access database known as HERB. Over 18,000 records have been examined so far, and of these, about 1 in 8 (2095) had to be annotated, due to either misidentification or changes in nomenclature. Thus, in some cases, historical records of species occurrences have turned out to be inaccurate and species distributions have been corrected accordingly. Ranges have been expanded for some species: the survey resulted in the discovery of about ten new state records, including mare's tail (*Hippuris vulgaris*) in Massachusetts and bigseed alfalfa dodder (*Cuscuta indecora*) in Rhode Island. The ranges of other species have turned out to not be as extensive as previously thought: specimens of bayberry willow (*Salix myricoides*) were misidentified in all but one Maine county (Aroostook), and the recognition of hybrid *Lycopodiella* species means that species such as Marguerite's clubmoss (*L. margueritiae*) now have more restricted distributions.

The next step for the Herbarium Recovery Project is the delivery of the data from the HERB database to New England's Natural Heritage Programs. Field surveys will continue, to keep current species distributions up to date. Arthur ended his talk by pointing out the need for continued revision of *Flora Conservanda* and by noting additional rare species that require field and herbarium surveys to ascertain their status in New England. During the question and answer session that followed his talk, Arthur made note of the fact that herbaria are on the decline and would benefit by being credited by any author who found them to be critical for the work published in a manuscript.

—Jennifer Forman, Recording Secretary.

CHECKLIST FOR CONTRIBUTORS TO *RHODORA*

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- Type manuscript on one side only of 8½ inch × 11 inch paper. Leave a 1-inch margin on all sides. Use a standard 12-pitch font type throughout the manuscript, including tables and appendices.
- Do not justify the right margin. Avoid hyphens or dashes at the right margin.
- The manuscript should be fully double-spaced throughout, including title, author's names and addresses, Literature Cited, appendices, tables, and figure legends.
- Each page of the manuscript; excluding page 1 but including Literature Cited, tables, appendices, and figure legends; should be numbered in the upper right-hand corner.
- Correct accents, umlauts, and other diacritical marks should be included. Where appropriate, multiplication symbol must be used rather than the letter x.
- Only names at the rank of genus and below are italicized or underlined. If underlining is used, do not underline spaces or punctuation.
- Special typefaces (italics, bold) should not be used except where indicated in this checklist.
- Do not italicize common Latin words, abbreviations, or phrases (e.g., et al., i.e., etc).
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Introductory Material

- **Running head** should be centered, at top of page, in upper and lower case letters include author's surname (if two authors use the word "and": use "et al." for more than two authors), long dash, and short title. Total characters, including spaces, must not exceed 44.
- **Title** should be centered, in upper and lower case. Only the first word of the title and proper nouns should be capitalized. Do not include authors of scientific names. Include family name in parentheses unless genus studied is type for the family.
- **Author(s) name(s) and professional address(es)** should appear below title, centered, in upper and lower case. Consolidate lines where possible. Two-letter postal abbreviations should be used for states. "Current address." should appear on a separate line immediately following address if author has moved, not as a footnote. If more than one author at an address, designate current address of author who has moved using a superscript number Include e-mail address(es) on a separate line following postal address(es). The first author will be considered the corresponding author unless indicated otherwise by a superscript number. The "Author for correspondence" statement follows on a separate line below the address, not as a footnote.
- **Abstract** must be one paragraph The abstract should be a concise statement of intent, methods used, results, and significance of findings. Do not cite references or taxonomic authors, or use and define abbreviations in the abstract. The word "Abstract" should be indented, in all capital letters, followed by a period, and should appear on the first line of the abstract.
- **Key Words** are used in indexing and should be chosen with that purpose in

mind. The title "Key Words" should appear at the left margin, followed by a colon. Only proper nouns should be capitalized.

Text

- The following are examples of first-level headings, which should appear centered and in all capital letters: MATERIALS AND METHODS, RESULTS, DISCUSSION, TAXONOMIC TREATMENT. The introduction is not titled in *Rhodora*. Do not combine results and discussion without first consulting with the Editor. Do not use a separate section for conclusions or summary; these must be incorporated into the discussion.
- Second-level headings should be indented, bold, upper and lower case, followed by a period, and should appear on the same line as the subsequent text. The text should be written such that additional levels of headings are not used.
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- Literature is cited in the text as follows:
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  2. Two authors: Angelo and Boufford (1996) or (Angelo and Boufford 1996).
  3. More than two authors: Mathieson et al. (2000) or (Mathieson et al. 2000).
  4. Note that there is no comma separating author and date.
  5. When more than one paper is cited at a time, they should be listed alphabetically by first author rather than chronologically [e.g., Angelo and Boufford (1996), Hill (1982), Mathieson et al. (2000)].
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  7. Manuscripts accepted but not yet published: Tryon (in press) or (Tryon, in press).
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- References to companies manufacturing products used in a study should not appear in the Literature Cited. Rather, the company name and location should be given in parentheses within the text [e.g., SYSTAT (SPSS, Chicago, Illinois)].
- When included, authors of scientific names should be cited either at their first usage in the text or in a table or appendix (e.g., in a flora or table of voucher specimens). It should be indicated which taxonomic treatment, revision, or flora nomenclature follows. Use standard abbreviations for author's names found in http://www.rbgkew.org.uk/data/authors.html or *Authors of Plant Names* by R. K. Brummitt and C. E. Powell.
- Names of publications cited in the text should be in italics.
- Avoid abbreviations in the text unless indicating measurement, then use a period unless abbreviating a metric term. Other abbreviations should be defined when first used [e.g., Scanning Electron Microscopy (SEM)]. Herbarium acronyms should follow

http://www.nybg.org/bsci/ih/ or *Index Herbariorum*, most recent edition.
- Numbers one through nine should be written out in the text unless a measurement or part of a taxonomic description. No comma is used with 4-digit numbers. A number should always precede a decimal point (e.g., 0.15).
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Taxonomic Treatments
- Use boldface Roman type for new names and new combinations, followed by "*sp. nov.*", "*comb. nov.*", etc.
- For nomenclatural history (i.e., synonymy and typification) use one paragraph per basionym [e.g., *Binomial* author, literature citation. TYPE: collection information from least-to-most-specific, *collector(s) collection number* (Holotype: herbarium acronym; Isotypes: herbarium acronym(s).].
- Exclamation points are used for type specimens examined, and types not seen are indicated as such (e.g., GH!, MO not seen).
- Lectotype designations are included together with an indication of where they were designated, what year, and by whom. This reference is listed in the Literature Cited. If the author of the paper is making the lectotypification, the phrase "here designated" is included.
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- Designation of a new taxon should include a brief Latin diagnosis, rather than a full Latin description, which sets forth succinctly how the new taxon differs from its congeners.
- A full description, in English, should follow. This should be parallel with other descriptions at the same rank in the paper, and should not repeat information given in any description of the inclusive taxon (i.e., species descriptions should not repeat information characteristic of the genus, if also described in the paper). All measurements are metric. Hyphens are used for parenthetical extremes. A multiplication symbol is used where appropriate, rather than the letter x.
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- A high-quality line drawing or photograph of the type specimen, illustrating the diagnostic features, should be included for new taxa.
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- Standard abbreviations for authors of binomials should be used according to http://www.rbgkew.org.uk/data/authors.html or *Authors of Plant Names* by R. K. Brummitt and C. E. Powell.
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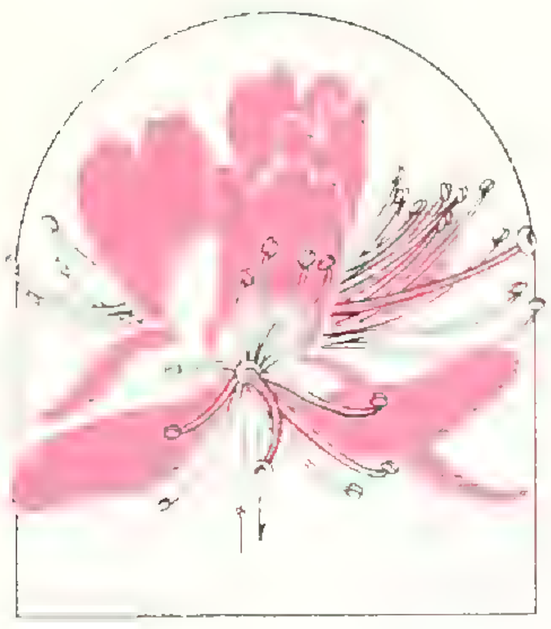

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PATTERNS OF PLANT INVASIONS AT SITES WITH RARE PLANT SPECIES THROUGHOUT NEW ENGLAND

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ABSTRACT. Although rare plant species are widely regarded as threatened by invasive plant species, few concrete data document the actual prevalence of invasives at sites with rare plant species. Data from comprehensive Conservation and Research Plans produced by the New England Wild Flower Society for 81 species of state-listed plants in New England provide quantitative information on the biogeographic distribution of invasive species where rare plants occur; their associations with multiple habitat variables and other threats; and hypothesized correlations with declines of rare plant populations. Eighteen invasive species were identified as co-occurring with rare plants; *Lythrum salicaria* was the most frequent and widespread. The spatial distribution of invasive species at rare plant sites paralleled large-scale patterns of both rare and invasive species richness and frequency throughout the region. However, invasive species occurred at only a subset of rare species sites, principally clustered along major rivers in New England. Connecticut reported the highest frequency and diversity of invasives, which declined with latitude. Invasives co-occurred with 38 (47%) of 81 rare species at 10.4% of 820 rare plant populations studied. For affected rare taxa, invasive species posed threats to a mean of 37.7% of their New England populations. Paired comparisons of invaded and uninvaded rare plant populations revealed a significant association of invasives with roads and with other anthropogenic threats. Populations of rare taxa in proximity to invasives showed higher (but statistically insignificant) rates of decline; classification analysis indicated that decline was best explained by the same habitat variables that were associated with invasive species presence, rather than by the presence of invasives alone. Thus, invasive species are both a direct threat and a symptom of larger landscape variables that influence the persistence of rare species.

Key Words: biogeography, invasive species, endangered plants, rarity, New England, conservation, invasibility

Invasive plant species are widely regarded as a significant threat to rare plant species, and may play a pivotal role in the endangerment of as many as half of all listed plants in the United States (Randall and Marinelli 1996; Westbrooks 1998; Wilcove et al. 1998). The general spatial distribution and impacts of invasive plant species in New England remain to be documented in detail (Farnsworth and Meyerson 1999a), although efforts are currently underway to identify invasives and to map their spread

(Mehrhoff et al. 2003). As yet, no data have been compiled specifically on the occurrence and effects of invasive plant species at sites with rare and listed plant species of the region. Concrete data are critical for understanding the scope and nature of invasions and for developing and justifying policies and management strategies to reduce their negative impacts on species of conservation concern. This paper analyzes detailed data on the presence and impacts of invasive species co-occurring with populations of 81 species of plants that are state-listed in one or more New England states. This data set has been collated from Conservation and Research Plans recently published by the New England Wild Flower Society, non-regulatory documents analogous in format and peer-review process to U.S. Fish and Wildlife Service Endangered Species Recovery Plans (Farnsworth 2003; New England Wild Flower Society 2003). Authors of plans collected these data from Natural Heritage Program Element Occurrence Records and their own observations of sites. These data provide a unique opportunity to:

1. map occurrences of invasive species, investigate biogeographic patterns, and pinpoint concentrations of invasions at particular types of sites where rare species occur;
2. identify which invasive species are most frequently impinging on rare species;
3. perform paired comparisons on invaded and uninvaded populations of rare plants to determine if invasions are associated with consistent environmental variables and/or with decline of rare plant populations; and
4. explore whether consistent differences exist among rare species for which invasive species are reported and those for which invasive species are not considered to be a threat.

MATERIALS AND METHODS

Data collection. The New England Plant Conservation Program (NEPCoP) of the New England Wild Flower Society initiated a five-year project in 1999 to complete comprehensive Conservation and Research Plans for 100 state-listed species. The species covered were chosen from over 300 taxa that were reviewed in the *Flora Conservanda* (Brumback and Mehrhoff, et al. 1996), and generally are listed as rare in one or more New England states. Each plan thoroughly reviews the taxonomy, ecology, biogeography, and conservation status of every known New England population of the rare taxon covered, and synthesizes the state of

the knowledge about each taxon throughout its entire range. Each plan then develops a set of quantitative, prioritized objectives designed to ensure the taxon's viability in New England throughout the next twenty years, based on its current status, its apparent habitat requirements, and the feasibility of alleviating threats and protecting populations at extant and new localities. Each plan stipulates specific actions, including monitoring, protection activities, management, *ex situ* collection, and scientific studies, that will meet these objectives. Plans are subjected to three rounds of rigorous, extra- and intramural peer review, in which they are evaluated for accuracy, clarity, internal consistency, and feasibility (cf. criteria of Brigham et al. 2002; Hoekstra et al. 2002). To date, 80 such plans have been published, covering 81 species. In writing these plans, authors frequently visited sites of extant rare plant occurrences to update information on population numbers and threats, including the presence of invasive species. Where site visits were not possible, information was summarized from previously existing Element Occurrence Records from each state's Natural Heritage Program. The data documented in field forms have been compiled by professional botanists or trained volunteer monitors (usually working with the New England Plant Conservation Program) who have visited sites, quantified population sizes of the target rare taxa, and described threats to population viability including the presence of invasive plant taxa within close proximity. The data have been meticulously collected. Field forms are standardized and call for the same type and quality of data from state to state, and the field observations of *in situ* threats to rare species show strong concordance among years and observers (Farnsworth, unpubl. data). Field forms have been assessed carefully for consistency and quality-control prior to being entered into Natural Heritage or NEPCoP databases. The data also have been critically evaluated by authors and reviewers of the Conservation Plans. However, it must be acknowledged that any data taken by a range of observers will necessarily be subject to observational bias and variability among individuals.

Based on data compiled for each plan, the following variables were entered into a table containing information on all 81 species covered to date [rows corresponded to individual Element Occurrences (EOs)]: Species; Family; County; Town(s); Date of First Observation; Date of Latest Observation; Population Status (actual or estimated numbers of ramets or genets at each time of survey); Description of Habitat; and Threats to the Taxon at the Site. A list of the rare species included in the data set is given in Table 1. For the purposes of this analysis, confirmed historic and extirpated EOs were excluded (invasive species had not been

Table 1. List of 81 state-listed plant species included in the analysis. Species with one or more populations affected by invasive species are given in bold-face type. "Invasive Species" column number codes correspond to the invasive species (listed in Table 2) that were identified as associated with the corresponding rare species; numbers in brackets denote the number of extant populations affected by invasives/ the total number of extant populations.

Species	Family	Invasive Species
Echinodorus tenellus (Mart.) Buchenau	**Alismataceae**	1 [1/1]
Taenidia integerrima (L.) Drude	**Apiaceae**	2,6,7,8,18 [7/10]
Zizia aptera (A. Gray) Fernald	**Apiaceae**	3,4,6,9 [2/3]
Aristolochia serpentaria L.	**Aristolochiaceae**	2,5 [2/12]
Asclepias purpurascens L.	**Asclepiadaceae**	3 [1/5]
Ageratina aromatica (L.) Spach	Asteraceae	[0/5]
Doellingeria infirma (Michx.) Greene	**Asteraceae**	2 [1/3]
Eupatorium leucolepis (DC.) Torr. & A. Gray var. *novae-angliae* Fernald	Asteraceae	[0/17]
Hasteola suaveolens (L.) Pojark.	**Asteraceae**	4,9 [1/1]
Hieracium robinsonii (Zahn) Fernald	Asteraceae	[0/1]
Liatris scariosa Willd. **var. *novae-angliae*** Lunell	**Asteraceae**	3,8,9 [6/77]
Nabalus serpentarius Pursh	Asteraceae	[0/10]
Polymnia canadensis L.	**Asteraceae**	10 [1/3]
Sclerolepis uniflora (Walter) Britton, Sterns & Poggenb.	**Asteraceae**	12 [1/2]
Solidago rigida L.	**Asteraceae**	3,6,8,9 [2/6]
Symphyotrichum concolor (L.) G.L. Nesom	Asteraceae	[0/6]
Cynoglossum virginianum L. var. *boreale* (Fernald) Cooperr.	Boraginaceae	[0/8]
Hackelia deflexa var. *americana* (A. Gray) Fernald & I.M. Johnst.	Boraginaceae	[0/19]
Neobeckia aquatica (Eaton) Greene	**Brassicaceae**	1,12,14 [2/4]
Moehringia macrophylla (Hook.) Fenzl	Caryophyllaceae	[0/16]
Paronychia argyrocoma (Michx.) Nutt.	Caryophyllaceae	[0/28]
Silene stellata (L.) W.T. Aiton	**Caryophyllaceae**	2,3 [1 /2]
Hypericum adpressum Barton	Clusiaceae	[0/14]
Carex atherodes Spreng.	Cyperaceae	[0/2]
Carex barrattii Schwein. & Torr.	Cyperaceae	[0/2]

Table 1. Continued.

Species	Family	Invasive Species
Carex davisii Schwein. & Torr.	**Cyperaceae**	2,3,5,6,7, 10,15 [5/8]
Carex garberi Fernald	Cyperaceae	[0/27]
Carex polymorpha Muhl.	Cyperaceae	[0/15]
Carex richardsonii R. Br.	Cyperaceae	[0/1]
Carex wiegandii Mack.	Cyperaceae	[0/34]
Cyperus houghtonii Torr.	Cyperaceae	[0/16]
Rhynchospora capillacea Torr.	**Cyperaceae**	1,4,8,11,15 [6/8]
Rhynchospora inundata (Oakes) Fernald	Cyperaceae	[0/10]
Rhynchospora nitens (Vahl) A. Gray	Cyperaceae	[0/13]
Schoenoplectus etuberculatus (Steud.) Sojak	**Cyperaceae**	4 [1/1]
Scirpus longii Fernald	**Cyperaceae**	1,4,7 [4/28]
Eriocaulon parkeri B.L. Rob.	**Eriocaulaceae**	1 [1/40]
Desmodium cuspidatum (Muhl.) Loudon	Fabaceae	[0/8]
Oxytropis campestris (L.) DC. var. *johannensis* Fernald	Fabaceae	[0/6]
Senna hebecarpa (Fernald) Irwin & Barneby	**Fabaceae**	5 [1/6]
Corydalis flavula (Raf.) DC.	**Fumariaceae**	5 [1/4]
Hydrophyllum canadense L.	**Hydrophyllaceae**	2,5,17 [3/5]
Juncus vaseyi Engelm.	Juncaceae	[0/6]
Agastache nepetoides (L.) Kuntze	Lamiacaeae	[0/2]
Agastache scrophulariifolia (Willd.) Kuntze	Lamiaceae	[0/4]
Scutellaria integrifolia L.	**Lamiaceae**	3 [1/ 2]
Chamaelirium luteum (L.) A. Gray	**Liliaceae**	5,6 [2/11]
Triantha glutinosa (Michx.) Baker	Liliaceae	[0/39]
Linum sulcatum Riddell	Linaceae	[0/2]
Diphasiastrum sitchense (Rupr.) Holub	Lycopodiaceae	[0/9]
Rotala ramosior (L.) Koehne	**Lythraceae**	1 [2/9]
Rhexia mariana L.	Melastomataceae	[0/9]
Pterospora andromedea Nutt.	**Monotropaceae**	7 [1/3]
Ludwigia polycarpa Short & Peter	**Onagraceae**	1,11 [2/10]
Ludwigia sphaerocarpa Elliott	**Onagraceae**	1,4 [2/6]
Botrychium lunaria (L.) Sw.	Ophioglossaceae	[0/4]
Amerorchis rotundifolia (Banks *ex* Pursh) Hultén	Orchidaceae	[0/7]
Goodyera oblongifolia Raf.	Orchidaceae	[0/13]
Listera auriculata Wiegand	Orchidaceae	[0/13]

Table 1. Continued.

Species	Family	Invasive Species
Listera australis Lindl.	Orchidaceae	[0/3]
Listera convallarioides (Sw.) Nutt.	Orchidaceae	[0/8]
Listera cordata (L.) R. Br.	**Orchidaceae**	1 [1/8]
Triphora trianthophora Rydb.	Orchidaceae	[0/23]
Oxalis violacea L.	**Oxalidaceae**	3,4 [2/16]
Panicum flexile (Gatt.) Scribn.	Poaceae	[0/2]
Sphenopholis nitida (Biehler) Scribn.	**Poaceae**	8 [1/9]
Polemonium vanbruntiae Britton	Polemoniaceae	[0/10]
Potamogeton ogdenii Hellquist & Hilton	**Potamogetonaceae**	12,14 [2/6]
Stuckenia filiformis (Pers.) Borner subsp. *occidentalis* (J.W. Robbins) R.R. Haynes, D.H. Les & M. Král	Potamogetonacae	[0/4]
Adiantum viridimontanum C.A. Paris	Pteridaceae	[0/7]
Hydrastis canadensis L.	**Ranunculaceae**	2,3,5,6,10 [3/7]
Ranunculus lapponicus L.	Ranunculaceae	[0/8]
Trollius laxus Salisb.	Ranunculaceae	[0/6]
Rosa acicularis Lindl. **subsp. *sayi*** (Schwein.) W. H. Lewis	**Rosaceae**	2 [1/5]
Populus heterophylla L.	**Salicaceae**	2,5 [1/7]
Saururus cernuus L.	**Saururaceae**	1 [1/3]
Castilleja coccinea (L.) Spreng.	**Scrophulariaceae**	1,5 [1/8]
Mimulus moschatus Douglas	**Scrophulariaceae**	2,13 [4/16]
Pedicularis lanceolata Michx.	**Scrophulariaceae**	1,4,7,16 [5/7]
Valeriana uliginosa (Torr. & A. Gray) Rydb.	**Valerianaceae**	4,13,15 [3/18]
Verbena simplex Lehm.	Verbenaceae	[0/3]

noted as the direct cause for any local extinction in the data set and verified, current information on extant populations was preferred). Also excluded were equivocal EOs for which invasive species were noted only as "nearby" or a "potential threat." Observers categorized invasive species as actual threats to rare taxa when strong evidence of direct competition (shading, physical smothering, etc.) was seen. The resulting data set contained 820 EOs. In a small proportion of cases (16%), sites were observed over several years, and the expansion of invasives or competitive exclusion of a rare species could be unambiguously documented. For this subset of populations for which unambiguous data were available, population decline (as a binary variable, decline or not) could be surmised from inspection of population levels at multiple

sampling dates. For the majority of cases, however, these observations represent a static and necessarily qualitative assessment of the impacts of invasive plants on the rare taxon, gathered by trained botanists. To date, these are the only data available; long-term, experimental studies of interactions between invasive and rare plants have not been conducted in New England.

Data analysis. Taxa classified as "Invasive" or "Likely Invasive" by the Massachusetts Invasive Plant Working Group (2003) were used to delimit the list of invasive taxa examined in the plans; this list encompasses all of the most common species identified as invasive by Natural Heritage Programs and other botanists throughout New England. Species nomenclature follows this list; however, since not all authors distinguished individual species of bush honeysuckles (*Lonicera* spp.), these were grouped as a single taxon. Because precise coordinates do not exist for all EOs, and to preserve confidentiality of exact locality information, occurrences of invasive species at rare species sites were mapped at the town polygon level using Geographic Information Systems software (ArcView 3.2, ESRI, Redlands, CA). To compare distributions of invasive species at rare species sites with the overall biogeographic distribution of invasive species, data were pooled by county (the best resolution currently available) and compared to data from county-level maps published in Magee and Ahles (1999) showing the presence/absence of invasive species.

I tested the hypothesis that, within species, populations with one or more invasive species present would differ consistently from populations without invasive species reported in terms of the following variables:

1. Habitat type, 11 classes coded: land in agriculture; coastal plain pond; upland field; floodplain; lacustrine; outcrop/summit/talus; power line right-of-way; rich woods; acidic rocky woods; wetland (wet meadow; marsh; bog; swamp); railroad.
2. Other identified threats, 16 classes coded: agriculture; collection/harvesting; natural disturbance including flooding, tidal overwash, treefalls, etc.; trampling; vulnerability to drought; dumping; erosion; eutrophication; herbicide application; herbivory; alterations in hydrology; logging; mowing; road construction; natural succession; or none.
3. Proximity to roads: yes if within 100 m; no if farther away.
4. Site protection status: 1 if owned or managed by a conservation organization; 0 if not.

5. Evidence of decline among sampling years: yes; no (from the subset of cases with multi-year data on plant population size).

Additional landscape variables examined included: circumneutral soils (yes, no), proximity to foot trails (as with roads), and an index of light availability (1 = shade to 5 = full-sun habitats). However, none of these additional variables explained variance in the model, so only the five categorical variables listed above were used in the analysis.

For the subset of 37 species with both invaded and uninvaded sites, invaded EOs were paired with uninvaded EOs according to geographic proximity (i.e., EOs were paired with EOs of the same species occurring in the same town or county) to control for variability in environmental factors such as climate and underlying bedrock. Sign tests were performed on the above variables using SYSTAT 8.0 for Windows (SPSS Inc., Chicago, IL) to test the null hypothesis that each of the variables above would not differ consistently by invasion status.

Another data set was used to compare among rare plant taxa with one or more invaded populations (N = 38 species) with those that had no such threats reported at any site (N = 43 species). This unpaired comparison tested whether consistent differences in the above variables characterized invaded versus uninvaded taxa (using classification tree analysis and inspection of frequency tables). The above variables were coded as a single "archetypal" case that broadly characterized the EO, based on inspection of each EO and a tabulation of the status of the majority of cases. For example, if the majority of EOs occurred in close proximity to a road or were declining between observation dates, these variables were coded as 1. The most frequent habitat type and threats characteristic of the majority of EOs were also used. Likewise, I examined the number of populations now regarded as "historic" or "extirpated" for each species, as a proportion of all populations recorded since the species was first documented in New England, testing the hypothesis that species with invaded populations showed a higher frequency of population loss than uninvaded species.

Categorical classification tree analysis using a Gini Index fitting method was run in SYSTAT to model the dependence of the response variable ("invaded" yes or no for either populations within taxa, or among invaded and uninvaded taxa) on this suite of categorical variables. Similar models were constructed to investigate the dependence of the variable "decline" (yes or no) on invaded status and the above variables. Classification analysis is analogous to a dichotomous botanical key, in which taxa are split into groups based on morphological or other variables

(Gotelli and Ellison, 2004). It is a very useful method for analyzing data in which the explanatory variables (analogous to characters in a key) can be either categorical or numerical, or which contain missing values (De'ath and Fabricius 2000). Classification trees repeatedly split the data (in this case, distinguishing "invaded" and "uninvaded" cases) into smaller categories, where each split depends on a single variable. Each split results in two groups, one containing a majority of "invaded" cases, the other containing a majority of "uninvaded" cases. The splitting continues until no further improvement in the statistical fit of the model can be attained, and the endpoint is as homogeneous as possible (i.e., each terminus contains as close as possible to 100% of the "invaded" or the "uninvaded" cases). An impurity index (based on the Gini Index) can be calculated to describe the reliability with which the model distinguishes among the categories of cases. For example, if the splitting variables successfully separate all of the "invaded" cases from the "uninvaded" cases, an impurity index of zero results. Predictive capacity of the model decreases as the impurity index increases. A proportional reduction in error (PRE) score indicates the proportion of variance in the data explained by the model as a whole.

RESULTS

Thirty-eight (47%) of the 81 rare species studied had one or more invasive species present at one or more populations (Table 1). Eighty-five (10.4%) of 820 populations studied had one or more invasive species present. For the subset of rare plant species that co-occurred with invasives, invasives posed threats to a mean of 37.7% (±27%, SD) of populations. The species classified as "invaded" fell into 27 families (Table 1). Ten families (Boraginaceae, Clusiaceae, Juncaceae, Linaceae, Lycopodiaceae, Melastomataceae, Ophioglossaceae, Polemoniaceae, Pteridaceae, and Verbenaceae) had no rare species with invasive occurrences. Families with multiple species experiencing invasions included the Apiaceae, Asteraceae, Cyperaceae, Onagraceae, and Scrophulariaceae. Invasive species themselves hailed from 16 plant families, only six of which overlapped with the 37 total rare families recorded here (Lythraceae, Poaceae, Brassicaceae, Fabaceae, Asteraceae, and Apiaceae).

Eighteen invasive taxa were identified as occurring at rare species sites (Table 2), with 110 total instances tabulated. *Lythrum salicaria* (purple loosestrife) was both the most frequent invasive species mentioned at rare species sites (with 20 occurrences region-wide) and the most widespread

Table 2. Invasive taxa identified as occurring at rare species sites. Second column reports the total number of occurrences throughout New England. Numbers in the column under each state abbreviation indicate numbers of invasive occurrences reported.

Species	Total	CT	MA	VT	NH	ME	RI
1. *Lythrum salicaria* L.	20	6	8	3	1	2	
2. *Berberis thunbergii* DC.	14	3	7	4			
3. *Celastrus orbiculatus* Thunb.	10	7	3				
4. *Phragmites australis* (Cav.) Trin. *ex* Steud.	9	3	3			1	2
5. *Rosa multiflora* Thunb.	9	6	3				
6. *Lonicera* spp.	9	5		4			
7. *Rhamnus cathartica* L.	8		2	5	1		
8. *Cynanchum louiseae* Kartesz & Gandhi	6	4		1			1
9. *Elaeagnus umbellata* Thunb.	4	3					1
10. *Alliaria petiolata* (M. Bieb.) Cavara & Grande	4	2	1	1			
11. *Polygonum cuspidatum* Siebold & Zucc.	4		1	2	1		
12. *Myriophyllum spicatum* L.	3	1		1	1		
13. *Tussilago farfara* L.	3		1		1	1	
14. *Trapa natans* L.	2		1	1			
15. *Frangula alnus* P. Mill.	2	1				1	
16. *Microstegium vimineum* (Trin.) A. Camus	1	1					
17. *Aegopodium podagraria* L.	1			1			
18. *Robinia pseudoacacia* L.	1			1			
TOTAL SPECIES		12	10	11	5	4	3
TOTAL OCCURRENCES	110	42	30	24	5	5	4

species (occurring in 5 of 6 New England states). *Berberis thunbergii* (Japanese barberry), *Celastrus orbiculatus* (oriental bittersweet), *Phragmites australis* (common reed), and *Rosa multiflora* (multiflora rose) followed in frequency (Table 2). Obviously, these invasive species are more widespread in New England than the number of occurrences reported here; our focus here is restricted to sites from which both rare and invasive species are known to co-occur.

Connecticut reported the highest number of invasive species at rare plant sites overall, with 42 occurrences (and a total of 12 invasive species) noted statewide. Massachusetts was second, followed by Vermont, New Hampshire, Maine, and Rhode Island (Table 2). The frequency of invasive species occurrences at rare plant sites largely

paralleled the longitudinal pattern of invasive species richness recorded in Magee and Ahles (1999), with concentrations of invasives in the southwestern and western regions of New England and richness declining from southwest to northeast (Figure 1). The number of invasive species occurrences per state at rare species sites was positively, but not significantly correlated with the mean number of invasive species reported per county by Magee and Ahles ($r^2 = 0.501$, but $P = 0.116$ due to a low sample size of 6 states). A positive correlation also existed between the number of invasive occurrences at rare species sites in a county and the number of rare species occurrences reported per county ($r^2 = 0.280$, $P = 0.005$), indicating that sites with high frequency and richness of rare species exhibited somewhat more frequent invasions.

Clusters of sites with rare plant species and co-occurring invasive species became evident when the data were mapped at the town level for New England (Figure 1). In large part, this distribution reflected "hot spots" of rare plant occurrences. However, invasive species occurred only at a subset of rare species sites across the region. Rare species co-occurred with invasive species particularly frequently along major water courses, including the Connecticut River, Housatonic River, and Lake Champlain; the St. John River in northern Maine also had an isolated invasive species report at a rare plant station. Rare and invasive species also tended to co-occur in regions of New England distinguished by circumneutral soils derived from alluvium and/or calcium-rich bedrock, particularly along the Stockbridge marble belt of western Connecticut, Massachusetts, and Vermont and traprock basalts of the Metacomet Range in west-central Massachusetts and Connecticut. Because rare plant species are less frequently found in proximity to dense population centers in New England, invasive species were not clustered around cities in this data set, even though their frequency in general tends to correlate positively with human population density.

For a subsample of 37 species with both invaded and uninvaded populations, paired comparisons were performed between neighboring populations with and without invasive species present (N = 63 site comparisons). Sign tests indicated that invaded populations were associated significantly and more frequently with nearby roads ($\chi^2 = 3.72$; df = 1, $P = 0.05$). Classification analysis yielded a model that separated invaded and uninvaded sites first by a suite of threats more frequently associated with invaded sites: dumping, hydrological alteration, eutrophication, trampling, herbicide use, succession, drought, erosion, and natural disturbance (Figure 2). For populations facing these

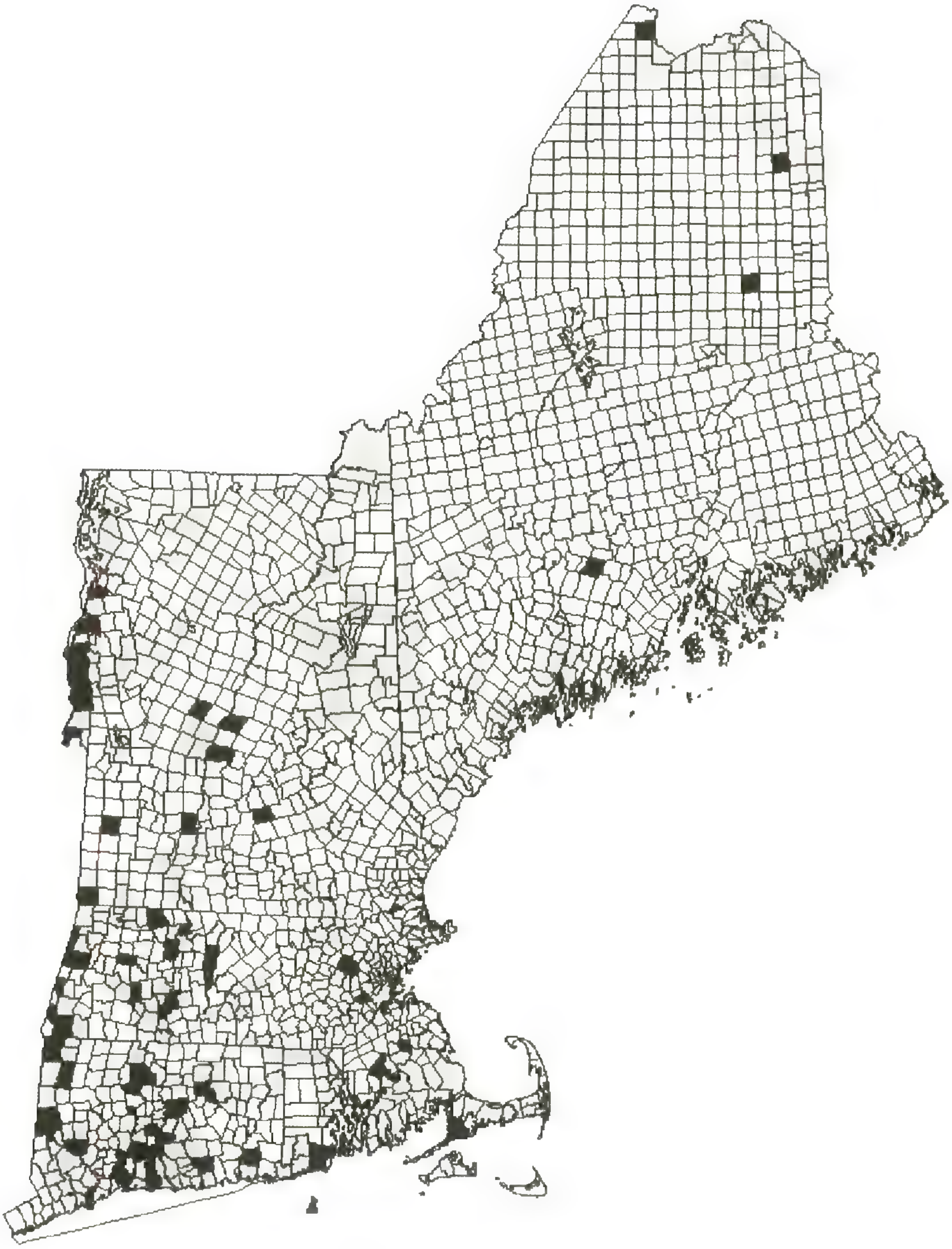

Figure 1. Map of New England states showing town boundaries. Gray fill indicates towns that had one or more occurrences of the rare species covered in the Conservation and Research Plans but had no invasives occurring at rare species stations within the town. Black shading indicates towns in which rare species were recorded as co-occurring with invasive species at particular sites. Towns with no fill had no rare species sites recorded from the Conservation and Research Plans; thus, no co-occurring invasives are recorded for these towns on the map, even though they may very well exist in these towns.

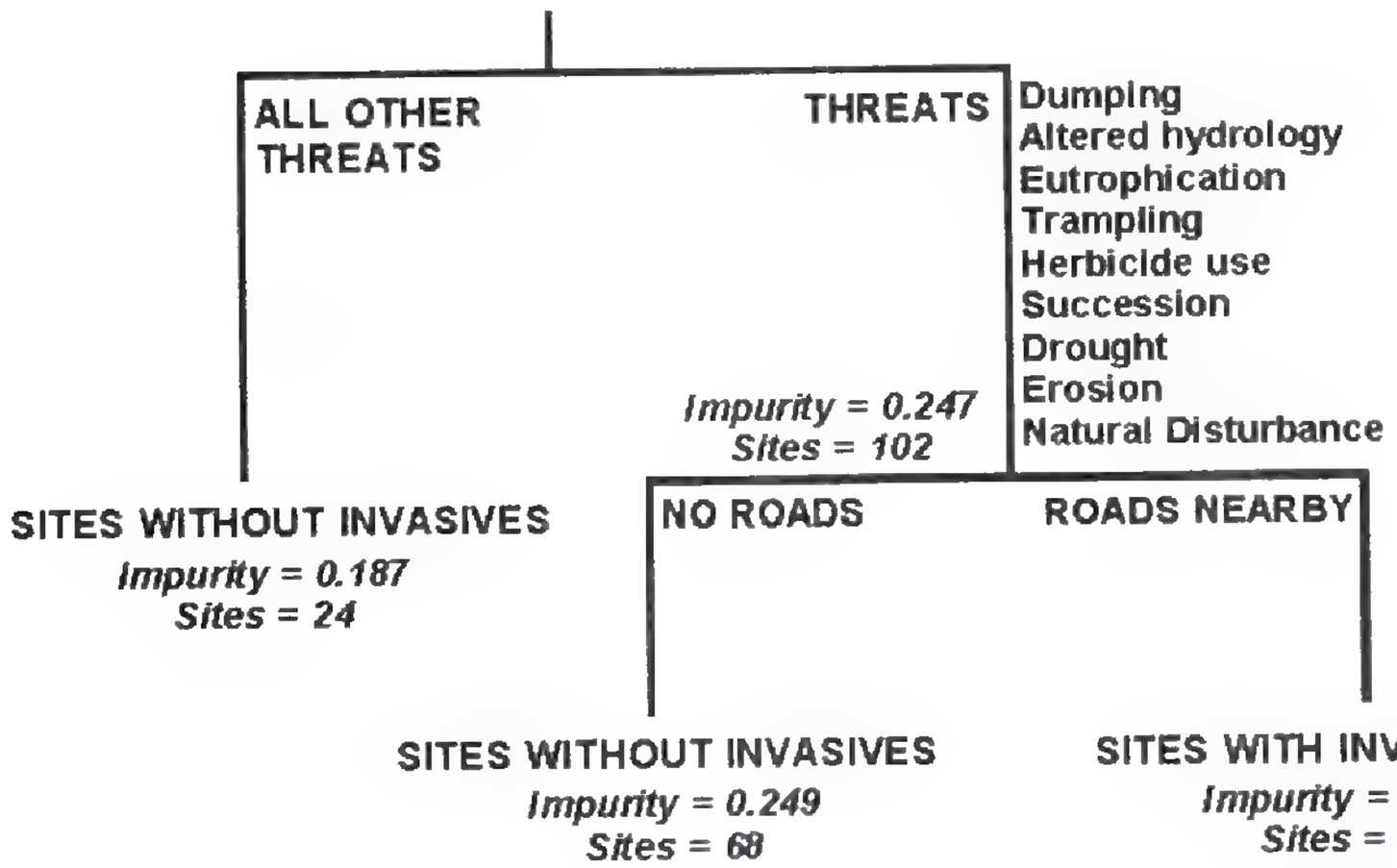

Figure 2. Classification tree on categorical data showing the variable states that best distinguish invaded and non-invaded sites (N = 126 total cases). Each node shows the number of cases (sites) that were split into "uninvaded" and "invaded" categories by each splitting variable: the impurity level at each node is proportional to the number of cases that were misclassified. The first bifurcation occurred on a suite of threats, which are listed at the node. The second bifurcation was on presence or absence of nearby roads. Overall model PRE was 0.109.

threats, invasion probability was higher among those in close proximity to roads (second bifurcation in Figure 2).

Invaded populations also tended to show marginally but not significantly more frequent declines in population numbers ($\chi^2 = 2.78$; df = 1, $P = 0.07$). The mean population size of invaded populations was 706 (±249 SE), approximately half that of uninvaded populations (1423 ± 849), but these differences were not significant by paired *t*-test due to high variance. The overall loss of rare plant populations (EOs) from historical levels (based on herbarium collections) to the present was also compared among species that co-occurred with invasive species and those that did not. Species with invasives suffered a higher proportion of populations lost (56.6% ± 0.04 SE of original populations gone) than uninvaded species (43.1% ± 0.05 of original populations gone), indicating a possible correlative link between prevalence of invasives and local extinctions ($t = 1.959$, $P = 0.054$). However, loss of populations was not correlated significantly with the number of sites invaded per species (by Pearson correlation). Likewise, classification analysis (data not shown; PRE = 0.211) did not separate EOs with declining populations from those showing no decline on the basis of invasion status. Rather, population decline was associated primarily with particular habitat types (specifically, anthropogenic habitats including

railroad and power line rights-of-way and old fields) and secondarily with small starting population sizes (< 14 plants per EO).

Classification tree analysis was also used to identify environmental factors associated with species with invasive co-occurrences and species not experiencing invasive threats (Figure 3). Invaded species were more frequently associated with particular types of threats, including mowing, natural disturbance, herbivory, erosion, collection, and eutrophication. Within species that faced additional threats, those occurring in lakes and lake shores, rich woods, and former agricultural sites exhibited lower rates of invasion than those of other habitats. Within the suite of species not associated with additional threats, a higher frequency of invasion was observed in sites under conservation protection than in unprotected areas.

DISCUSSION

Despite half a century of research on the characteristics and impacts of invasive species (Elton 1958), and a broad recognition that invasive species are a leading factor in the endangerment of rare species (Wilcove et al. 1998), we still have few data that specifically document the prevalence of invasive species at rare species sites. Studies that characterize distributions of invasive species at landscape or regional scales are few (Grice et al. 2000; Higgins et al. 1999; Huebner 2003; Kalkhan and Stohlgren 2000; Lockwood et al. 2001; McKinney 2002; Pysek et al. 2002); none have been attempted as yet for New England, and none have addressed multiple rare species. Data collected as part of a comprehensive conservation planning process by the New England Wild Flower Society provide a unique opportunity to quantify the co-occurrence of invasive and rare species and to begin to describe the impact of invasions on listed taxa. Such analyses are critical to justify efforts to regulate activities that contribute to invasive species spread. In order to prioritize management efforts, we also need to understand which invasive species pose the greatest threats, which rare species are most vulnerable, and what environmental factors are associated with invasions (Elias 1987; Hobbs and Humphries 1995).

The data set presented here covers 81 rare plant species for which detailed site observations have occurred. This is a subset, albeit a sizable one, of the total number of rare species listed in New England, and can only imperfectly represent the state of our knowledge about the true distribution of these rare species in the region. Data like these are necessarily somewhat biased by collecting and surveying trends and are artifacts, to a certain extent, of the preferences of botanists for focusing

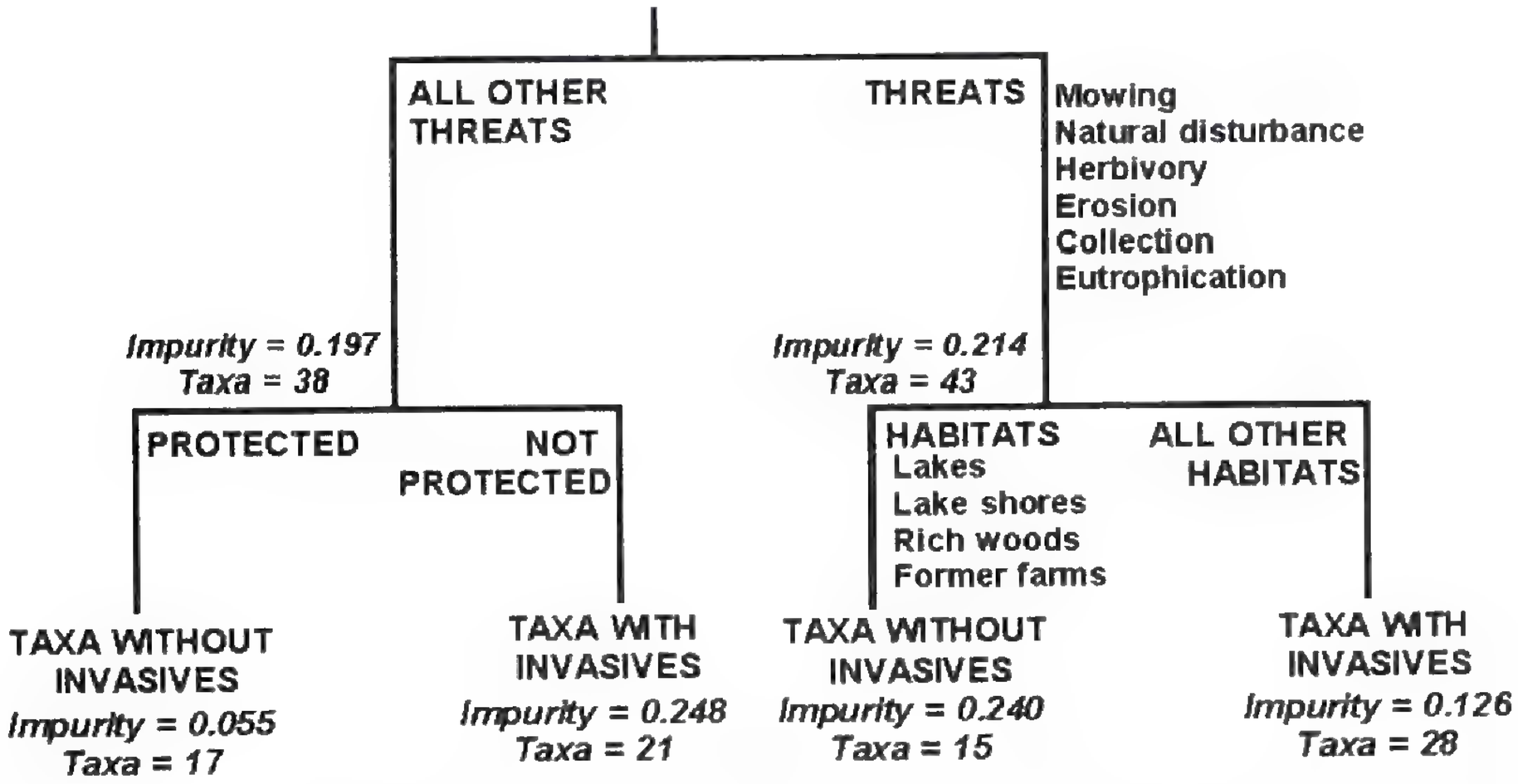

Figure 3. Classification tree showing the variable states that best distinguish species that exhibited co-occurring invasives and those that were free of invasives (N = 81 species). Numbers of taxa at each node show the number of cases that were split into "uninvaded" and "invaded" categories by each splitting variable. The first bifurcation was on the presence of all threats (see text for details). Bifurcations then proceeded on protection status (held or not held by a conservation entity) and habitat type (listed in the figure). Misclassification rates (impurity levels) ranged from 0.055 to 0.248 at each node. Overall model PRE was 0.347.

rare plant searches in particular areas. However, New England is among the most thoroughly botanized regions of North America, and recent efforts both to reverify and collate data from herbarium specimens (the Herbarium Recovery Project of NEPCoP) and to train hundreds of plant surveyors to recognize and document both rare and invasive species (the Plant Conservation Volunteer Program and the Invasive Plant Atlas of New England) have yielded some of the most complete information available for any region on the distribution and status of rare and invasive plant species. The data presented here lay the foundation for future, more targeted surveys to determine which rare plant stations are most vulnerable to invasive species and for long-term studies that document the actual ecological effects of invasives on the viability of rare plant populations. There already exist examples from management-oriented trials in which removal of an invasive species has a demonstrably positive impact on a target rare taxon or natural community (i.e., The Nature Conservancy Wildland Invasive Species Team 2003), including some trials addressing species covered in the NEPCoP Conservation Plans. However, the majority of these trials remain anecdotal or unpublished, and scientific results from adaptive management need to be circulated much more widely. The restoration successes and negative

effects of management to remove invasive species from rare species localities should be carefully and critically monitored over a minimum of several years and the findings published and widely disseminated (e.g., Farnsworth and Meyerson 1999b; Manchester and Bullock 2000; Stylinski and Allen 1999).

These analyses demonstrate that invasive plant species co-occur with nearly half (47%) of the 81 rare species studied. This accords in magnitude with large-scale estimates for 1055 state- or federally-listed plant species in the United States, of which 57% were viewed as affected by alien species (Wilcove et al. 1998). For the rare species with reported invasions, an average of more than one-third (37.7%) of their populations had an invasive species present, representing a substantial potential impact on the viability of each of these taxa as a whole in New England. The data suggest that the presence of invasive species may be correlated with both losses of populations (local extinction) and declines in population size. However, declines also tended to reflect larger environmental variables (such as anthropogenic disturbance of habitat) that may themselves simply facilitate colonization by invasive species at the same time as they harm rare species. Much more detailed experimental studies are needed to tease apart the precise impacts of invasive species from a host of complex factors that impinge on population viability. The list of invaded species (Table 1) offers a suite of taxa on which such studies could be focused.

Invasive species co-occurred with rare plants principally along major New England watercourses, including the Connecticut and Housatonic rivers and Lake Champlain (Figure 1). In part, this reflects the geographic distribution of rare species aggregations in New England (e.g., Massachusetts Natural Heritage and Endangered Species Program 2001), but the concentration along rivers represents only a subset of the rare species "hot spots" in the region (Farnsworth 2003). For example, other regional "hot spots" of rarity were relatively free of invasives, including the White Mountains of New Hampshire, interior Maine, and Cape Cod. Such a distribution also reflects the overall species richness of invasive species in western and southern counties of New England (Magee and Ahles 1999), which provide a source pool for new invasions (*sensu* Zobel 1997). The majority of invasive species identified in this study tend to be especially common in floodplains or mesic uplands with rich alluvial soils. Rivers and streams can transport floating seeds directly and can act as corridors for dispersal by animals (Stohlgren et al. 1998). Likewise, changes in hydrology—particularly dampened flooding intensity and frequency –can create artificially stable conditions

for invasive species along river shores (Decamps 1993; Galatowitsch et al. 1999).

Invasions at rare plant sites also tended to occur somewhat more frequently in counties with higher richness and density of rare species. A correlation between invasion frequency and local rare species richness accords with emerging hypotheses that species-rich communities may be more vulnerable to invasions than species-poor assemblages (Kalkhan and Stohlgren 2000; Levine 2000; Levine and D'Antonio 1999; Lonsdale 1999; Pysek et al. 2002; Stohlgren et al. 1999; but see Kennedy et al. 2002). In part, this may result from higher availabilities of resources, including water and nutrients, which favor growth of both rare and invasive species (Stohlgren et al. 1999). Disturbances that transiently release resources, such as eutrophication events, also can favor invasions (Burke and Grime 1996; Davis et al. 2000); in fact, eutrophic sites were associated more frequently with invasions in the present study (Figure 2).

I tested the hypothesis that invasions of rare plant species sites might be more frequently associated with certain habitat variables that promote introduction and establishment of alien propagules. Proximity to roads, for example, has been positively correlated with frequency of invasive species because tires and intentional plantings can transport seeds (e.g., Coleman 2003), disturbance from road construction creates colonization sites (e.g., Harrison et al. 2002; Watkins et al. 2003), and road maintenance practices (i.e., salt usage) favor persistence of invasives over non-invasive species (e.g., Richburg et al. 2001; Wilcox 1989). The model presented here did distinguish invaded sites from uninvaded sites on the basis of nearness to a road (Figure 2). Interestingly, proximity to foot trails was not associated with higher rates of invasion, even though people and animals (e.g., deer) can be sources of introduced seeds along these routes (Vellend 2002).

Habitat disturbance was a significant factor distinguishing invaded and uninvaded populations, and invaded and uninvaded species (Figure 2, 3). Ill-timed mowing, natural disturbances, herbivory, erosion, trampling, dumping, and drought were threats commonly associated with invasions. Disturbance has long been viewed as an important driver in invasions of plant communities (Hobbs and Huenneke 1992; Sher and Hyatt 1999). It is of interest that communities with rare species that occupied areas under conservation protection showed a slightly higher proportion of invasions than those of unprotected sites (Figure 3). This may reflect a higher reporting rate of invasions for these sites by managers, or higher rare species richness and invasibility of protected areas; these hypotheses need to be teased apart in future studies.

Invasive species are both agents and symptoms environmental change. This regional analysis has important implications for the management of both rare and invasive species. Three invasive species accounted for 40% of all invasions at rare species sites in New England (Table 2): *Lythrum salicaria*, *Berberis thunbergii*, and *Celastrus orbiculatus*. These taxa should be targeted for more precise, quantitative studies of their distribution and impacts (e.g., Farnsworth and Ellis 2001). Many invasive species are concentrated in southern and western New England, and rare species with more boreal distributions may currently fall at the northern edge of several invasives' ranges. However, new invasions will have to be watched for in remote northern areas, particularly as climatic warming ensues. Management for invasive species will also have to take into account a complex suite of other interacting environmental factors that influence rare species persistence and decline.

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JALTOMATA ANDERSONII (SOLANACEAE): A NEW SPECIES OF PERU

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ABSTRACT. *Jaltomata andersonii* (Solanaceae), here named, is distributed on the western slope of the Andes, in the Departments of Ancash and Lima, Peru, from 2300 to 3400 m of elevation. This species differs from others of the genus by having an unarticulated axis connecting the flower to the plant where all others have both a peduncle and a pedicel. The following combination of features also characterize this species: the hairs of leaves and axes are gland-tipped; the petiole is no longer than 1 cm; the flowers are solitary; the corolla is broadly crateriform-rotate, purple, and up to 3.7 cm in diameter; and the filaments are extremely villous at their bases.

Key Words: Andes, flora of Peru, *Jaltomata andersonii*, Solanaceae

The genus *Jaltomata* Schltdl. includes about 45 herbaceous and shrubby species divided into two subgroups. The purple/black-fruited subgroup (six species) comprises perennial herbs having rotate corollas, and is distributed from Arizona, U.S.A. to Bolivia. The orange and red-fruited subgroup (39 species) includes shrubs having rotate, crateriform, infundibular, tubular, or urceolate corollas, and occurs on continental South America except for two species, one of the Galápagos Islands and the other of the Greater Antilles. The purpose of this paper is to report a new species of the Peruvian Andes discovered during fieldwork in 1998.

Mione and Coe (1992) placed the following binomials in synonymy with *Jaltomata aspera* (Ruiz & Pav.) Mione: *Saracha ciliata* Miers, *S. lacrima-virginis* Bitter, and *S. urbaniana* Bitter & Dammer. The type specimens of all of these binomials have a single relatively large flower per inflorescence, and were collected either on the west slope of the Andes or in the lomas [a fog-fed desert habitat of the west coast of

South America having a high level of endemism (Dillon 1997)]. The new species here described also has a single flower per inflorescence and is from the west slope of the Andes. Given these similarities, one may wonder if one of the aforementioned binomials represents the earliest name of the species here described.

None of the above binomials represent the earliest name of this species for the following reasons. The type specimens of the above *Saracha* binomials have both a peduncle and a pedicel, and were described as producing red nectar. According to the protologue of *Jaltomata aspera* (Ruiz and Pavón 1799) the type was collected in Amancaes and the flower is violet in the middle ("in centro violacea"). Amancaes is located within lomas habitat, and is within several hundred meters of sea-level [according to a specimen label of *J. aspera* collected at Amancaes (*Weberbauer 5246a*, US), and Dillon, Field Museum of Chicago, pers. comm.]. The description of the flower as violet in the middle suggests that the type produced red floral nectar, and red floral nectar has been documented for *J. aspera* (Vilcapoma S. and Granda P., Universidad Nacional Agraria La Molina, pers. comm.). In contrast, the species here described has a single unarticulated axis joining the flower to the plant (Figure 1A), lacks red nectar, and grows at high elevations, not in the lomas habitat. Thus, all of the above *Saracha* binomials are synonyms of *J. aspera*, as originally reported (Mione and Coe 1992).

TAXONOMIC TREATMENT

Jaltomata andersonii Mione, *sp. nov.* TYPE: PERU. Dept. Lima: prov. Huarochirí, highway from Lima to La Oroya between km 82 & 83, 2500 m, with *J. propinqua* (Miers) Mione & M. Nee, 16 Jan 1998, *T. Mione, S. Leiva G. & L. Yacher 622* (HOLOTYPE: NY!; ISOTYPE: CONN!). Figure 1.

Herba perennis usque ad 20 cm alta, petiolo usque ad 1 cm longo, foliis et axibus pilos digitiformes, glanduliferos apice ferentibus, flore solitario, corolla purpurea, late crateriformi-rotata usque ad 3.7 cm cruciatim, filamentis maxime villosis basi.

Much branching, presumably perennial, herb to 20 cm, the hairs of the younger axes and leaves gland-tipped. Leaves alternate, sometimes geminate, the blades ovate, 4–7.5 cm long (to 10.5 cm on *Spooner et al. 7364a*) × 2–3.5 cm wide, 3–4 pairs of primary veins, the apex often somewhat acuminate, the base usually cuneate and symmetrical or

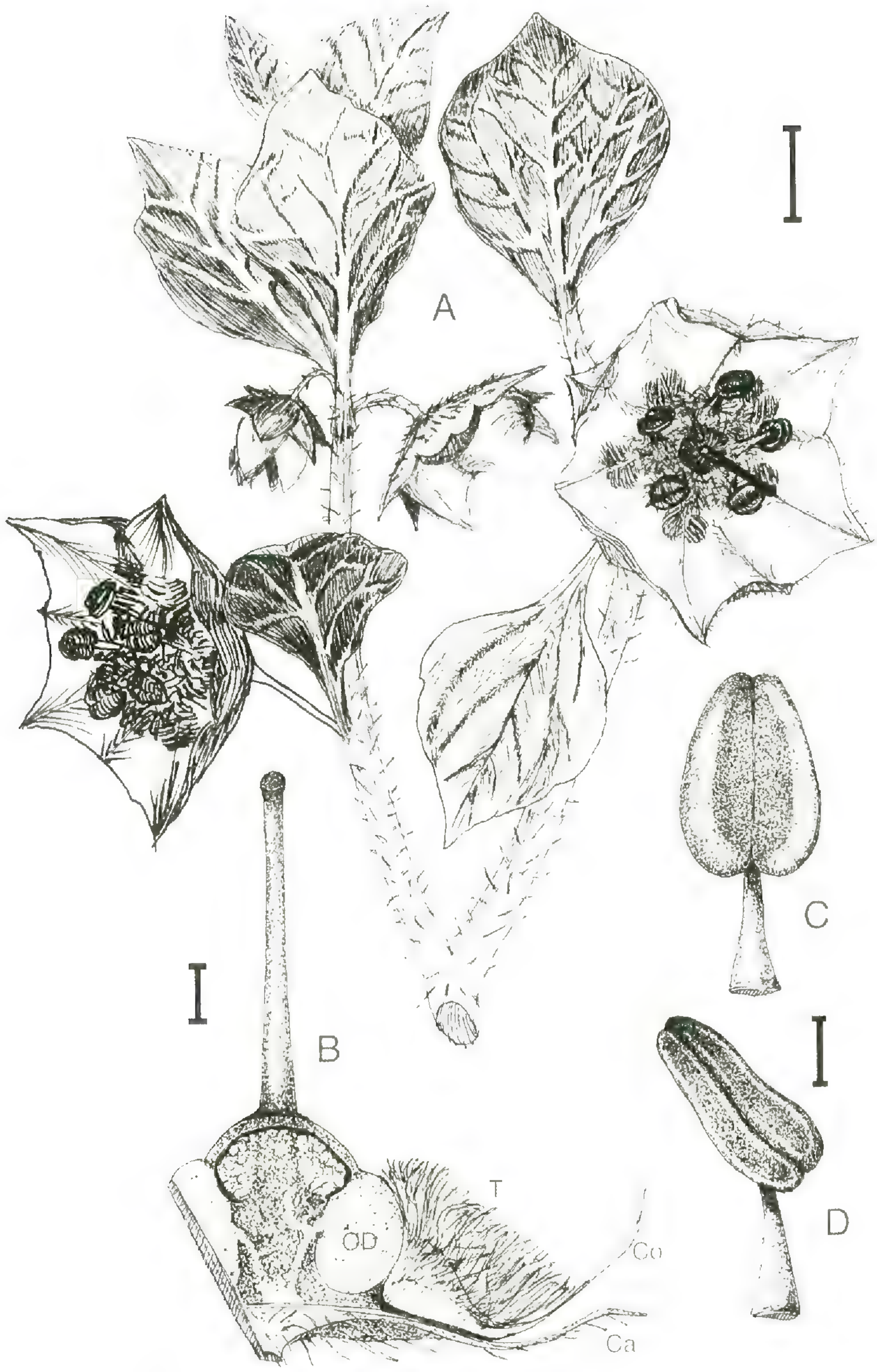

Figure 1. *Jaltomata andersonii*. A. Branch with flowers and leaves; B. Partial flower, longitudinal hand-section with lower left excised, Ca – calyx, Co – corolla, OD – ovarian disk, T – trichomes at base of stamen, the stamen otherwise removed; C and D. Anther and part of filament, dorsal and lateral views, respectively. Bar = 1 cm in A, and 1 mm in B and C. Drawn by Luis Serazo from *T. Mione, S. Leiva G. & L. Yacher 620*.

nearly so, adaxially densely pilose due to erect finger hairs, abaxially sparsely pubescent (nearly glabrous on *Laudeman 5365*), the margin nearly entire to sinuate-dentate, ciliate, the petiole to 1 cm long. Peduncle unarticulated, villous, 13–18 mm long; flower solitary. Calyx green, rotate, 16–21 mm across at anthesis, the lobes triangular with an acute apex, abaxially with a raised costa, bearing gland-tipped finger hairs to 3 mm long, and stalked multicellular glands (illustrated in Mione and Serazo 1999) 85–100 μm long, adaxially with a uniform covering of erect, glandless hairs 0.24–0.3 mm long, the margin with two classes of hairs: gland-tipped finger hairs to 2.8 mm long and glandless hairs to 0.1 mm long; calyx to 25 mm across with fruit. Corolla broadly crateriform-rotate, 5-lobed (Figure 1A), to 3.7 cm in diameter, purple with 5 pairs of dark-green maculae in a proximal ring, each pair of maculae straddling the main vein that extends radially to the tip of a corolla lobe, closing for the night, the margin ciliate, with glandless finger hairs to 0.6 mm long; both faces of corolla with abundant, evenly distributed stalked multicellular glands 85–100 μm long. Stamens 5, 6.9–7.2 mm long, filaments straight, extremely villous at base (Figure 1A, B); anthers (Figure 1C, D) 1.9–2.8 mm on pressed specimens, to 3.9 mm long on specimens preserved in alcohol in Peru, drying brown, or yellow if covered with pollen. Style straight (Figure 1B), 5.7–6.3 mm long, 0.15–0.36 mm wide at midlength. The stigma the same width as the distal end of the style, 0.21–0.3 mm wide (pressed), 0.36 mm wide (preserved in alcohol in Peru), both measured perpendicular to the length. Ovarian disk broad, girdling base of the ovary (Figure 1B). Gynoecium glabrous, except for stigma papillae to 13 μm long; ovary glabrous but appearing villous (Figure 1B) because of the dense vestiture of the stamen bases. Berries of unknown color, probably orange or red, 12 mm across (measured on *Laudeman 5365*).

SPECIMENS EXAMINED: PERU. Dept. Ancash: prov. Bolognesi, Chiquián, 3150–3400 m, cultivated grounds below the village, with *Agave americana* and *Mutisia*, 5 Feb–2 Apr 1997, *M. Weigend & N. Dostert 97/173* (F). Dept. Lima: prov. Cajatambo, Baños de Churin, 2591 m, among rocks, Feb 1946, *C. Laudeman 5365* (K); prov. Canta, Cuesta de Huamantanga, 10.8 km NW from the Lima to Canta road on the road to Huamantanga, 2720 m, 7 Apr 1999, *D. Spooner, A. Salas, R. Torres & R. Hoekstra 7364a* (herbarium of T.M., MOL not seen); prov. Huarochirí, Lima to La Oroya highway, at km 73 walk up to 2300 m of elevation, dry treeless hillside, sandy soil with rocks, with Cactaceae, *Carica candicans*, *Lycianthes* sp., and *Schinus molle*, 15 Jan 1998, *T. Mione, S. Leiva G. & L. Yacher 616* (NY), *S. Leiva G., T. Mione & L. Yacher 2122* (F, HAO); Lima to La Oroya highway, km 83, 2550 m, roadside with *Agave*, 16 Jan 1998, *T. Mione, S. Leiva G. & L. Yacher 620* (CONN), *S. Leiva G., T. Mione & L. Yacher 2127* (HAO).

DISCUSSION

Jaltomata andersonii is distributed on the west slope of the Andes, in the departments of Ancash and Lima, Peru. It grows in treeless, usually dry, rocky habitats. It flowers in January, February, and March. We did not interview local people about uses, but the fruits may be eaten, given that ripe fruits of several other South American species of this genus are consumed (e.g., Mione and Coe 1996; Mione and Serazo 1999; Mione et al. 2000, 2001).

Jaltomata andersonii is most similar to *J. aspera*. Both have one relatively large flower per inflorescence, and are much-branching, low-growing perennial herbs that occur on the western slope of the Andes. *Jaltomata andersonii* grows to a height of 20 cm, while *J. aspera* grows to 50 or 60 cm (pers. obs.; Ruiz and Pavón 1799). *Jaltomata aspera* has both a pedicel and a peduncle, the corolla is light green, filaments are either glabrous or very sparsely pubescent at base, red floral nectar is produced, and it grows from 200 to 2290 m of elevation. In contrast, *J. andersonii* has an unarticulated axis (by definition a peduncle, though the peduncle may have been lost by reduction) connecting the flower to the plant, the corolla is purple (brown and whitish green on *Weigend 97/173*), the filaments are extremely villous at their bases (Figure 1 A, B), red nectar is not produced, and it grows at elevations from 2300 to 3400 m. *Jaltomata aspera* grows both in the lomas and the Andes, while *J. andersonii* grows only in the Andes. Furthermore, the hairs of the leaves and stems of *J. aspera* are rigid and glandless [as observed on living plants of *Mione et al. 615;* described as hirsute by Macbride (1962)] while the hairs of *J. andersonii* are soft to the touch and gland-tipped (as observed on living plants of *Mione et al. 616, 620, & 622*). We were able to see both of these species in bloom during January of 1998 because of the rains associated with the El Niño event of 1997/1998.

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TAXONOMIC STUDIES IN THE MICONIEAE (MELASTOMATACEAE). VIII. A REVISION OF THE SPECIES OF THE *MICONIA DESPORTESII* COMPLEX ON HISPANIOLA

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ABSTRACT. The Hispaniolan species of *Miconia* section *Cremanium* with setose-serrate leaves (i.e., the *M. desportesii* complex) include *M. desportesii*, *M. tetrastoma*, *M. monciona*, and *M. sphagnicola*. Species descriptions, nomenclatural information, specimen citations, and eco-geographical characterizations for these species are presented, along with an identification key. These species occur from 800 to 2400 m elevation in moist montane forests, moist forests on limestone, cloud forests, and moist forests of *Pinus occidentalis*. All are endemic to Hispaniola and restricted in distribution except for *M. tetrastoma*, which is more widespread and also occurs in Cuba.

Key Words: *Miconia*, Melastomataceae, Hispaniola, endemics

Fieldwork conducted in Haiti and the Dominican Republic and a survey of herbarium material in connection with an investigation of the systematics of *Miconia* section *Chaenopleura* (DC.) Triana (Melastomataceae: Miconieae) have yielded numerous specimens of *Miconia* Ruiz & Pav. that belong to other sections of this large and diverse genus. These were carefully studied in connection with an investigation of generic and sectional limits within Miconieae (Judd and Skean 1991), and especially were used to clarify the monophyly of the Antillean species of section *Chaenopleura* (Judd, in prep.). The six Hispaniolan species of *Miconia* section *Cremanium* (D. Don) Naudin are united by androecial characters, and all but two are endemic to this island. It is, therefore, convenient to present here a taxonomic revision of a phenetically similar (and likely closely related) group of four species: the *M. desportesii* complex.

Miconia section *Cremanium* often has been confused with section *Chaenopleura* (Gleason 1958; Judd and Skean 1991), but the two groups are easily distinguished, at least in the Antilles. Species of *Miconia* section *Cremanium* have anthers that open by a gaping apical pore that sometimes is extended, forming a short to elongate, broadly to narrowly V-shaped longitudinal slit, with the septum between the anther sacs clearly visible and usually protruding; the anthers also often have bilobed

basal appendages. In contrast, the anthers of species of section *Chaenopleura* are more strongly obovate and open by two longitudinal slit-like pores (Cogniaux 1891; Judd 1994; Judd and Beaman 1988; Judd and Karpook 1993; Judd and Skean 1987, 1991, 1994a, b; Judd et al. 1988, 1995; Liogier 2000; Wurdack 1973, 1980). In both groups the stamens are the same color as the petals (frequently white) and are arranged radially (i.e., the androecium is actinomorphic). It is likely that some South American species of section *Chaenopleura* [e.g., *M. campii* Wurdack, *M. chionophila* Naudin, *M. bullata* (Turcz.) Triana, *M. latifolia* (D. Don) Naudin, *M. salicifolia* (Bonpl. *ex* Naudin) Naudin, and *M. cernua* Naudin; see also Gleason 1958; Judd and Skean 1991] are taxonomically misplaced; these have the anthers opening by gaping apical pores that are characteristic of section *Cremanium*. More study of sectional delimitations within *Miconia* certainly is needed. However, the distinctions in anther morphology outlined above consistently distinguish the species treated here from those of section *Chaenopleura*, which at least in the Greater Antilles is a large and diverse group and likely constitutes a clade (Judd, in prep.) based on both morphological and molecular data.

SECTION *CREMANIUM* ON HISPANIOLA, WITH EMPHASIS ON THE *MICONIA DESPORTESII* COMPLEX

Although the monophyly of section *Cremanium*, as currently circumscribed, is unclear, most of the species with enlarged to gaping anther pores that occur on Hispaniola do appear to be closely related. Four of the species of section *Cremanium*, here called the *Miconia desportesii* complex, share the following conditions: 1) usually narrowly paniculate to racemose inflorescences, 2) leaves setose-serrate, 3) indumentum of abaxial surface of the lamina of only minute globular hairs, the variably stellate hairs restricted to major veins, and 4) twigs with two opposing faces slightly concave, and these positioned above the point of petiole attachment at adjacent proximal node. These species are *M. desportesii*, *M. tetrastoma*, *M. monciona*, and *M. sphagnicola*. In addition, all but one of these species have distinctive seeds with a roughened seed coat, the outer layer of which is composed of isodiametric, bulging cells. *Miconia desportesii* has seeds with a smooth testa.

Within this group, *Miconia sphagnicola* and *M. monciona* may be sister species; both share the putative apomorphic characters of very small leaves (i.e., 4–25 × 2–9.5 mm) and a low to prostrate habit (i.e., shrubs not over 1 m tall). *Miconia sphagnicola* is especially distinctive because of its large, somewhat ellipsoid, red fruits. The mature fruits of

M. tetrastoma and *M. desportesii* are smaller, more or less globose, and blue or blue-black. Unfortunately, mature fruits have not been collected in *M. monciona* (although the immature fruits clearly are globose). *Miconia desportesii* may be most closely related to *M. monciona* and *M. sphagnicola*. *Miconia desportesii*, *M. sphagnicola*, and *M. monciona* have fairly narrow inflorescences with 0–4 major branch pairs, with the proximal segment of the lowermost branches (when present) 2.5–17 mm long, the flowers in 3- to 5-flowered glomerules, and each anther opening by a single large pore, often extending into a short notch or V-shaped longitudinal slit, with the septum between the anther sacs clearly visible, dividing the opening in half. Their narrowly paniculate to racemose inflorescences and glomerulate flowers may be synapomorphic.

Miconia tetrastoma, on the other hand, is very distinctive, because its stems have elongate-branched, irregularly stellate, dendritic, to globular-stellate hairs that are roughened-granular (due to bulging, papillae-like, and thin-walled cells) and often disintegrating. The stellate hairs of *M. desportesii*, *M. monciona*, and *M. sphagnicola* are more or less smooth (i.e., lack these thin-walled, bulging cells). *Miconia tetrastoma* also differs in the structure of the anther pore, resulting in a pore with four (instead of two) openings, as reflected in its specific epithet. The flowers in this species are in dichasia and are well separated from each other. It is of interest that pouch-like mite-domatia have evolved, probably independently, in *M. desportesii* (where they are always present) and in *M. tetrastoma* (where they are of variable occurrence).

In contrast to the species discussed above, a poorly known species from the Massif de la Hotte, Haiti, which should be placed in section *Cremanium* (based on its anthers, which have a large apical pore, with an evident, but not protruding septum), lacks the features outlined above for the *M. desportesii* complex (see also key). This species, known in the literature as *Ossaea alloeotricha* Urb., is not considered further here. It is the subject of a separate study in which it is provided with a detailed description and transferred to *Miconia*, along with a more detailed consideration of its relationships (Judd et al., 2004).

A final species of section *Cremanium* on Hispaniola is the distinctive *Miconia tetrandra* (Sw.) D. Don *ex* G. Don. It is widely distributed on Hispaniola and grows throughout the Greater and Lesser Antilles (Cogniaux 1891). This species is phenetically divergent from members of the *M. desportesii* complex, especially in its larger and entire-margined leaves, indumentum of flattened-stellate hairs, and flowers with only four stamens (see key). The presumed Hispaniolan endemic, *M. abeggii* Urb. & Ekman [Ark. Bot. 22A (17): 35. 1929; based on a single

gathering: HAITI. Massif du Nord, Port Margot, Morne Maleuvre, 800–1000 m, 8 Dec 1924, *E. L. Ekman H21709* (S!)], is not distinguishable from *M. tetrandra*. It merely represents a vigorous sterile shoot, and is not separable in any feature from some vigorously growing plants of *M. tetrandra*. Leaf size in this widespread and common species ranges from 7–28 cm in length and 1.7–12 cm in width.

For convenience, *Miconia tetrandra* and *Ossaea alloeotricha* are included in the key, which thus includes all Hispaniolan members of *Miconia* section *Cremanium*. However, these species are not formally included in this taxonomic treatment as they are likely not closely related to the members of the *M. desportesii* complex.

A brief taxonomic review of the Hispaniolan species of *Miconia* section *Cremanium* with setose-serrate leaves (i.e., the *M. desportesii* complex) is provided below. The morphological variation evident within and between each is presented (see descriptions and key) along with a summary of their geographical ranges and habitat preferences.

MEASUREMENTS, TERMINOLOGY, AND COMMON CHARACTERS

All measurements (except plant height and flower and fruit color, which were taken from information given on specimen labels or observed in the field, and floral and fruit measurements, which were taken from liquid-preserved or rehydrated material) included in the key and descriptions of species come directly from dried herbarium material. Inflorescence length was measured from the terminal flower to the point at which the first branch-pair emerges from the axis, and the peduncle is defined as the internode separating the cyme from uppermost leaf pair. The prominent veins running in convergent arches toward the leaf apex are termed secondary veins since it is clear that they branch from the midvein.

All species of the complex have opposite and decussate leaves, although they often appear to be distichous in *Miconia sphagnicola*. The petals are white, glabrous, imbricate, and apically interlocking in bud, with the apex rounded, emarginate, with an asymmetrically located notch, and the margin entire. The stamens are white and glabrous. The style is straight, terete, glabrous, and slightly sunken into apex of ovary; placentation is axile.

KEY TO THE SPECIES OF *MICONIA* SECTION *CREMANIUM* ON HISPANIOLA

1. Leaf margin entire; hairs of abaxial surface flattened-stellate; stamens 4, equaling the number of petals; leaf lamina 7–28 cm long . . . . . *M. tetrandra*

1. Leaf margin serrulate or setose-serrate/serrulate; hairs of abaxial leaf surface dendritic to elongate-branched, globular-stellate or obscurely stellate, sometimes roughened (due to minute, papillae-like cells), along with minute globular hairs; stamens 8 or 10, twice the number of petals; leaf lamina 0.4–14.5 cm long . . . . . (2)
   2. Adaxial leaf surface with several rows of conical projections (at apices of bullations); indumentum of abaxial leaf surface with thick-stalked, irregularly dendritic to elongate-branched hairs, along with smaller globular-branched hairs and minute globular hairs; leaf margin serrulate, the teeth to 0.4 mm long, each lacking a terminal seta; young twigs quadrangular to terete; flowers 4-merous with ovary 2-loculate; proximal portion of filaments 1.1–1.4 mm long . . . . . *Ossaea alloeotricha*
   2. Adaxial leaf surface lacking conical projections (although it may be ± bullate); indumentum of abaxial leaf surface with minute globular hairs, with thin-stalked, irregularly to globular-globular stellate hairs and minute globular hairs on major veins (or in *M. tetrastoma*, of minute globular hairs, with thin-stalked, roughened and often disintegrating, ± obscurely stellate to dendritic hairs on midvein and secondary veins); leaf margin clearly setose-serrate, the teeth to 0.6–0.97 mm long, each terminated by a hair-like seta; young twigs with two opposing sides slightly concave; flowers 5-merous with ovary 3-loculate (but in *M. sphagnicola*, 4- or 5-merous, with ovary 2- or 3-loculate); proximal portion of filaments 1.25–2.7 mm long . . . . . (3) *M. desportesii* complex
      3. Stems with elongate-branched, irregularly stellate, dendritic, to globular-stellate hairs, these rough-granular (due to bulging, papillae-like, thin-walled cells) and often disintegrating, and with minute globular hairs; inflorescences with 3–8 major branch pairs, with proximal segment of lowermost branches 4–30 mm long, the flowers in dichasia, clearly separated; anther opening by a single large pore, with the septum between the anther sacs extending beyond the pore apex, dividing into four smaller pores . . . . . *M. tetrastoma*
      3. Stems with irregularly stellate to globular-stellate and elongate-branched hairs (the latter only at the nodes),

these lacking bulging, thin-walled cells, and with minute globular hairs; inflorescences with 0–4 major branch pairs, with proximal segment of lowermost branches (when present) 2.5–17 mm long, the flowers in 3- to 5-flowered glomerules; anther opening by a single large pore, often extending into a short notch or V-shaped longitudinal slit, with the septum between the anther sacs clearly visible, dividing the opening in half . . (4)

4. Leaves with pouch-like domatia on abaxial surface at junction of major secondary veins with the midvein; erect shrub 4 m tall; leaf base narrowly to widely decurrent; petals 1.3–1.9 × 0.8–1 mm; berry blue-black, 2–3 mm long; testa smooth . . . . . *M. desportesii*

4. Leaves lacking pouch-like domatia; ± erect to prostrate shrub to 1 m tall; leaf base acute to rounded; petals 1.7–3.6 × 1.2–2.2 mm; berry red, 5.6–8.4 mm long (in *M. sphagnicola*, but mature fruits not reported in *M. monciona*, in which they may reach 3.5 mm); testa roughened, with individual cells bulging . . . . . (5)

5. Leaves 4–13.3 × 2–5.75 mm, with one pair of secondary veins; petiole 0.6–2 mm long; low, often prostrate shrub, to 0.4 (–1) m tall, usually rooting along branches; flowers 4- or 5-merous; ovary 2- or 3-loculate . . . . . *M. sphagnicola*

5. Leaves 10–25 × 4.6–9.5 mm, with two pairs of secondary veins (one of these inconspicuous); petiole 1.3–5 mm long; shrub to 1 m tall, not rooting along branches; flowers 5-merous; ovary 3-loculate . . . . . *M. monciona*

TAXONOMIC TREATMENT

1. Miconia desportesii Urb., Symb. Antill. 8: 496. 1921. TYPE: DOMINICAN REPUBLIC. Prov. Barahona: inter brachia rivulorum Cañada maluca, 1600 m, Apr 1912 (fl), *Padre M. Fuertes 1491* (HOLOTYPE: B, presumably destroyed; ISOTYPE: NY!, here designated as a lectotype). Figure 1.

Shrub to 4 m tall. Indumentum of multicellular, ferrugineous, irregularly stellate to globular-stellate, and minute globular hairs. Young

Figure 1. *Miconia desportesii*, flowering, on road between San José de Ocoa and Valle Nuevo, Cordillera Central, Dominican Republic.

twigs ± rectangular in cross section, with two opposing faces slightly concave (i.e., those positioned above point of petiole attachment of adjacent proximal node) and the alternate faces slightly convex, 0.75–3 mm wide, becoming terete with age, the indumentum of moderate to dense multicellular, irregularly stellate to globose-stellate hairs, and minute globular hairs on the concave surfaces, becoming sparsely pubescent with age; nearly glabrous on the convex surfaces, with some

elongate-branched hairs at the nodes; internodes 3.25–25 mm long. Leaves with petiole 1.25–9.5 mm long, the indumentum sparse, similar to that of the twigs, to essentially glabrous; blade elliptic to ovate, sometimes narrowly so, 9.5–54 × 4.4–19 mm, flat, coriaceous, the apex acute to obtuse, the base narrowly to broadly decurrent, the margin distinctly serrate, at least distally (ca. proximal 20–60% of margin entire), plane to slightly revolute, the largest teeth to 0.1–0.6 mm, most narrowed to a slender apical portion having the form of a seta; venation acrodromous, distinctly suprabasal, with prominent midvein and 2 pairs of secondary veins, with 1 pair of conspicuous secondary veins placed 0.85–3.3 mm in from margin, with 1 pair of inconspicuous intramarginal secondary veins, and numerous percurrent tertiary veins oriented subperpendicular to midvein, the tertiary veins either connected by quaternary veins or separated by variously developed composite-intertertiary veins; adaxial surface green, usually drying dark brown, the indumentum essentially glabrous, but with a few minute globular or ± irregularly stellate hairs along midvein or major secondary veins, the midvein and major secondary veins slightly to strongly impressed, tertiary veins not to very slightly impressed, other veins not impressed, surface wrinkled and minutely papillose after drying because of the presence of scattered druse crystals; abaxial surface light green, sparsely to moderately covered with ferrugineous to reddish minute globular hairs, the midvein and major secondary veins prominently to moderately raised, all other veins ± flat; with a pair of pouch-like domatia 0.9–1.6 mm long, located at the junction of the major secondary veins and the midvein, occasionally with a second pair of domatia at the leaf base. Inflorescences terminal, several to many flowered, paniculate to racemose cymes of 2 or 3 major branch-pairs, 1.9–5.4 cm long, 1.4–2.6 cm across; proximal segment of lowermost inflorescence branches 3.2–12.3 mm long, distal internodes increasingly shorter, ultimate branches 0–0.6 mm, and flowers appearing in 3- (to 5-) flowered glomerules, terminating inflorescence branches, with a few hairs similar to those of the twigs; peduncle 6.1–15 mm, with similar indumentum; each inflorescence branch associated with a deciduous narrowly ovate to obovate or oblong bract, 3.5–14 × 0.5–3 mm, the apex acute to obtuse; flowers in dichasia, each subtended by 2 caducous narrowly elliptic to linear bracteoles 1–1.95 × 0.3–0.5 mm, the indumentum of a few minute globular or irregularly branched hairs, especially along margin, or glabrous, the apices acute to acuminate; the lowermost inflorescence branches sometimes in the axils of leaves. Flowers sessile or nearly so, the pedicel 0–0.5 mm long. Hypanthium cylindrical-orbicular, free

portion ca. 0.5–0.95 mm long, the outer surface with very sparse, ferrugineous, minute globular hairs, the inner surface glabrous and slightly ridged, with ridges extending at hypanthium apex as minute extensions. External calyx teeth 5, 0.1–0.22 × 0.7–1.1 mm, triangular, with acute to obtuse apex, indumentum glabrous; internal calyx lobes 5, 0.28–0.41 × 0.7–1 mm, triangular to ovate-triangular, pale green (?) to red, glabrous, the apex acute to rounded (shortly acuminate), the margin ± entire; calyx tube 0.1–0.2 mm long. Petals 5, ovate to obovate or oblong, 1.3–1.9 × 0.8–1 mm, glabrous, white to pink tinged, imbricate and interlocking in bud, with apex rounded, with an asymmetrically located notch; margin entire. Stamens 10, geniculate; proximal portion 1.25–1.7 mm long; distal segment (anther and distal portion of style) 1.5–2 mm long, the anther 1–1.15 mm long, with fertile portion of anther sacs 0.5–0.6 mm long, opening by a single, large, terminal pore, sometimes extending into a short ventral notch, with septum between the anther sacs clearly visible, the base slightly lobed, and with a dorsal, apically oriented projection ca. 0.06–0.16 mm long. Ovary 3-loculate (N = 8), ca. 2/3-inferior, globose to ovoid, 1.3–1.5 × 0.85–1.1 mm, glabrous, strongly ridged, and these ending in rounded apical projections, with crown to 0.55–0.75 mm encircling the base of style; style 2.35–3.15 mm long; stigma slightly expanded. Berries globose to ellipsoid, 2–3 × 1.85–3.1 mm, reddish when immature, turning blue-black, essentially glabrous. Seeds rounded-pyramidal, 0.94–1.57 mm long; testa with isodiametric cells, the surface smooth.

DISTRIBUTION AND ECOLOGY. *Miconia desportesii* is endemic to Hispaniola (the Dominican Republic) and occurs in the Cordillera Central and Sierra de Baoruco (Figure 2) in cloud forests and moist forests of *Pinus occidentalis* Sw. from 1600 to 2150 m elevation. Commonly associated melastomes include *M. selleana* Urb. & Ekman, *M. zanonii* Judd, Skean & R. S. Beaman, and *Tetrazygia urbaniana* (Cogn.) Croizat *ex* Moscoso. Other common associates are *Baccharis myrsinites* (Lam.) Pers., *Brunellia comocladiifolia* Humb. & Bonpl. subsp. *domingensis* Cuatr., *Buddleja domingensis* Urb., *Eupatorium illitum* Urb., *Fuchsia triphylla* L., *Garrya fadyenii* Hook., *Gaultheria domingensis* Urb., *Lobelia rotundifolia* Juss., *Lyonia buchii* Urb., *Myrica picardae* Krug & Urb., *Myrsine coriacea* (Sw.) R. Br. *ex* Roem. & Schult., *Rhytidophyllum auriculatum* Hook., and *Vaccinium racemosum* (Vahl) Wilbur & Luteyn.

SPECIMENS EXAMINED: DOMINICAN REPUBLIC. Prov. Azua [as Prov. La Vega]: Constanza, Loma La Vieja, ca. 2000 m, *E. L. Ekman H14056* (A, NY, S). Prov.

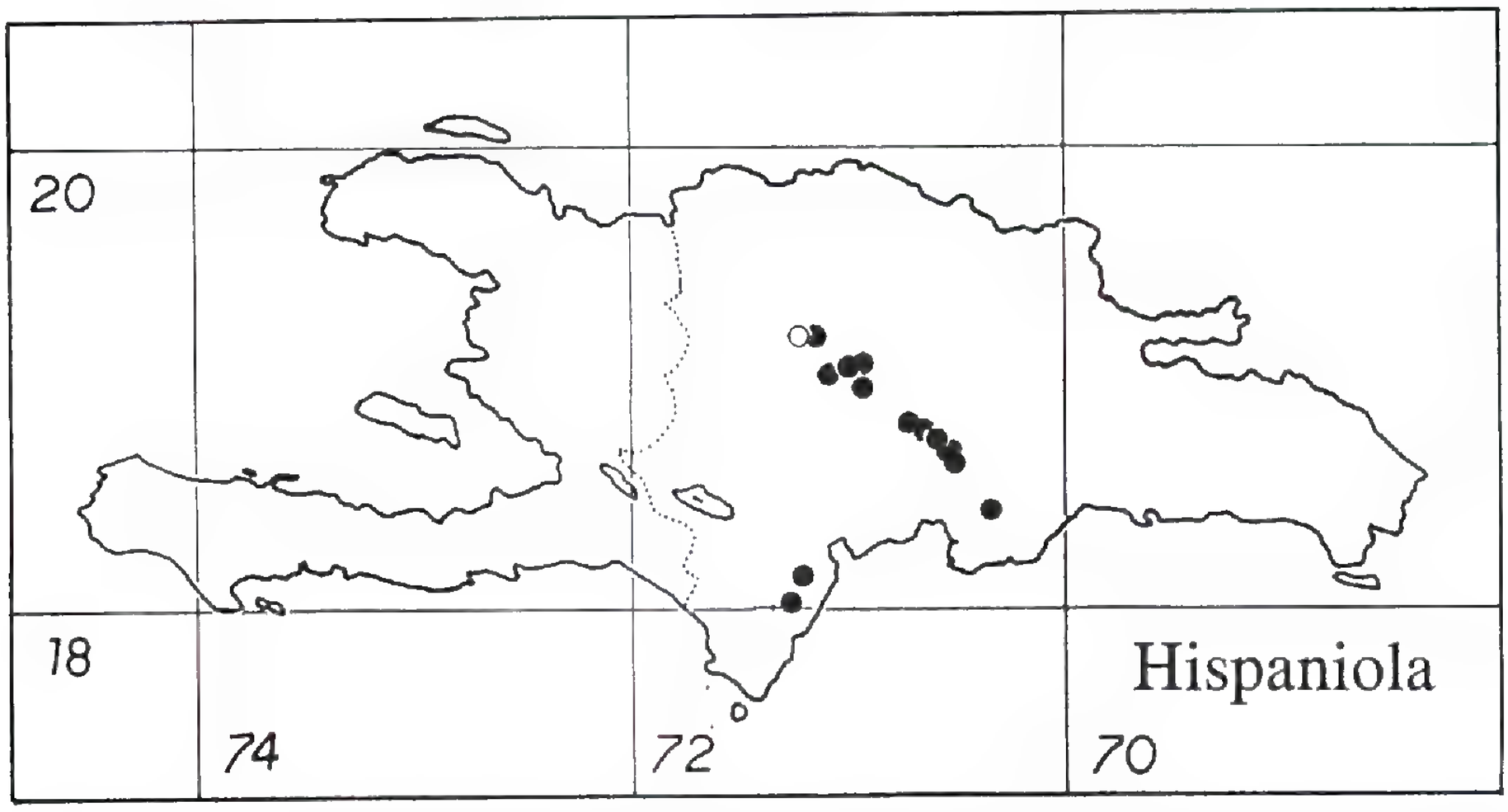

Figure 2. Distribution of *Miconia desportesii* (dots) and *M. monciona* (circle) on Hispaniola.

Barahona: Sierra de Bahoruco, on Loma Remigio, above El Burren de Aguas Blancas, and inland from La Cienaga de Barahona, 18°04′N, 71°12′W, 1150–1287 m, *T. A. Zanoni 42211* (FLAS). Prov. Peravia: Cordillera Central, N slope of Loma Valvacoa (Balbacoa), ca. 25 km WNE of San Cristóbal, 18°27.5′N, 70°21′W, 1630–1700 m, *F. Jiménez 837* (FLAS); La Horma Arriba, San José de Ocoa, 1800–2000 m, *A. H. Liogier 18598* (F, NY); 41 km from San José de Ocoa on rd. to Valle Nuevo, at "El Gelechar," La Nevera, 18°43′N, 70°36′W, 2400 m, *A. Veloz 1066* (FLAS). Prov. Santiago: Cordillera Central, Monción, high ridge between Río Magua and Río San Juán, 2100 m, *E. L. Ekman H12832* (GH, IJ, S, US); La Rucilla, 1800–2000 m, *A. H. Liogier 12143* (NY, US); La Cotorra to La Rucilla, 1900 m, *A. H. Liogier 21720* (NY, US); base of La Cotorra, 1110–2710 m, *E. Marcano* [*J. Jiménez No.*] *4820* (FLAS, US). Prov. La Vega: Cordillera Central, ca. 41.2 km S of Constanza (and 41.8 km N of San José de Ocoa) on rd. between San José de Ocoa and Valle Nuevo, 2150 m, *W. S. Judd 5108* (A, DUKE, F, FLAS, JBSD, MICH, MO, MSC, NY, S, US); La Nevera, from Valle Nuevo to San José de Ocoa, 2100 m, *A. H. Liogier 15495* (NY, US); La Cotorra, Ciénaga de Manabao, Jarabacoa, 1900 m, *A. H. Liogier 17204* (IJ, NY, US); La Nivera, Valle Nuevo, 2100 m, *A. H. Liogier 17994* (F, IJ, NY, US); Cordillera Central, along Rt. 41, 41.8 km N of San José de Ocoa, between San José de Ocoa and Valle Nuevo, 2150 m, *J. D. Skean 1735* (B, FLAS, JBSD, NY, S); Cordillera Central, Parque Nacional J. A. Bermúdez, "La Laguna," ca. 3 hours on foot from La Cienaga (de Manabo) along trail to Pico Duarte, 19°02′N, 70°32′W, 2000 m, *T. A. Zanoni 37478* (FLAS).

Miconia desportesii can easily be distinguished from the other species treated here by its leaves with decurrent bases, consistent presence of mite-domatia (abaxially, at junction of major secondary veins and midvein, and occasionally also at junction of minor secondary veins and midvein), smaller flowers (e.g., petals 1.3–1.9 mm long and 0.8–1 mm wide; anthers 1–1.15 mm long), and seeds with a smooth testa.

2. Miconia monciona Urb. & Ekman, Ark. Bot. 23A (11): 17. 1931. TYPE: DOMINICAN REPUBLIC. Prov. Monte Cristi [now the border between Prov. Santiago and Prov. San Juan]: Cordillera Central, Monción, high ridge between Rio Cenobi and Rio San Juán, ca. 1900 m, 11 Jun 1929 (fl), *E. L. Ekman H12807* (HOLOTYPE: S!; ISOTYPES: GH!, NY!, S!, US!).

Shrub to ca. 1 m tall. Indumentum of multicellular, ferrugineous, irregularly stellate to globular-stellate hairs, and minute globular hairs. Young twigs ± rectangular in cross section, with two opposing faces slightly concave (i.e., those positioned above point of petiole attachment of adjacent proximal node) and the alternate faces slightly convex, 1–2.5 mm wide, becoming terete with age, the indumentum of moderate to dense multicellular, irregularly stellate to globular-stellate hairs, and minute globular hairs, with some elongate-branched hairs at the node, becoming only sparsely pubescent with age; internodes 3–24 mm long. Leaves with petiole 1.3–5 mm long, the indumentum sparse to moderate, similar to that of the twigs; blade ovate to elliptic, 10–25 × 4.6–9.5 mm, flat, coriaceous, the apex acute, the base obtuse to rounded, the margin distinctly serrate, at least distally (ca. proximal 25–50% of margin entire), plane to slightly revolute, the largest teeth to 0.15–0.8 mm, most narrowed to a slender apical portion having the form of a seta; venation acrodromous, basal, with prominent midvein and 2 pairs of secondary veins, with 1 pair of conspicuous secondary veins placed 0.6–1.5 mm in from margin, with 1 pair of inconspicuous intramarginal secondary veins, and numerous percurrent tertiary veins oriented subperpendicular to midvein, the tertiary veins either connected by quaternary veins or separated by variously developed composite-intertertiary veins; adaxial surface green, sometimes yellowish after drying, the indumentum essentially glabrous, but with some ferrugineous, ± stellate hairs along midvein, the midvein strongly to moderately impressed, the major secondary veins slightly to very slightly impressed, minor secondary veins, tertiary and higher order veins not impressed, surface roughened and minutely papillose after drying because of the presence of numerous druse crystals; abaxial surface light green, sometimes yellowish after drying, moderately covered with reddish brown minute globular hairs, with a few globular-stellate hairs on midvein and major secondary veins, but these quickly deciduous, the midvein and major secondary veins prominently to moderately raised, all other veins ± flat. Inflorescences terminal, several-flowered, racemose cymes of 2 to 4 major branch-pairs, 2–4.5 cm long, 1–1.6 cm across; proximal segment of lowermost inflorescence branches 4–8 mm long,

distal internodes increasingly shorter, ultimate branches 0.3–1.1 mm long, and flowers appearing in 3- to 5-flowered glomerules, terminating inflorescence branches, with sparse to moderate hairs similar to those of the twigs; peduncle 1.25–2.1 cm long, with similar indumentum; each inflorescence branch associated with ± deciduous, narrowly obovate to oblong bract, 4.5–10 × 1–2.75 mm, the apex acute; flowers in dichasia, each subtended by 2 caducous narrowly obovate to linear bracteoles 2–3 × 0.5–0.9 mm, the indumentum of a few minute globular hairs, the apices acute; the lowermost inflorescence branches sometimes in the axils of leaves. Flowers sessile or nearly so, the pedicel 0–0.4 mm long. Hypanthium cylindrical-orbicular, free portion ca. 1–1.3 mm long, the outer surface with moderate, ferrugineous, minute globular hairs, the inner surface glabrous and not ridged. External calyx teeth 5, 0.4–0.85 × 0.9–1.3 mm, triangular, with acute to acuminate apex, indumentum of a few minute globular hairs, but frequently glabrous; internal calyx lobes 5, 0.5–0.72 × 0.9–1.1 mm, ovate-triangular, pale green to reddish, glabrous, the apex ± obtuse, the margin entire to minutely fimbriate; calyx tube 0.15–0.22 mm long. Petals 5, broadly ovate to obovate, 2.9–3.5 × 1.65–2.2 mm, glabrous, white to pink tinged, imbricate and apically interlocking in bud, with apex rounded, with an asymmetrically located notch; margin entire. Stamens 10, geniculate; proximal portion 1.8–2.2 mm long; distal segment (anther and distal portion of filament) 2.1–2.85 mm long, the anther 0.95–1.65 mm long, with fertile portion of anther sacs 0.8–1.25 mm long, opening by a single, large, terminal pore, often extending into a short slit, with the septum between the anther sacs clearly visible, the base slightly lobed, and with a dorsal, apically oriented projection ca. 0.25 mm long. Ovary 3-loculate (N = 5), ca. 3/5-inferior, ± globose, 1.4–2.1 × 1.25–1.9 mm, glabrous, ± ridged, and these ending in minute, rounded, apical projections, with crown to 0.7–0.9 mm encircling the base of style; style 4.5–5.3 mm long; stigma somewhat expanded. Berries globose, only immature fruits seen, and fruits possibly reaching ca. 3.5 × 2.5 mm when mature. Seeds rounded-pyramidal, ca. 0.75–1.1 mm long; testa ornamented with isodiametric, ± bulging cells.

DISTRIBUTION AND ECOLOGY. Endemic to the Dominican Republic, in the Cordillera Central, on ridge between Rio Cenobi and Rio San Juan (Figure 2), in pinelands (*Pinus occidentalis*), ca. 1900 m.

SPECIMENS EXAMINED: Only known from the type.

In their description Urban and Ekman (Urban 1931) compare this species with *Miconia desportesii*. The species is poorly known, and has

only been collected once, where it is evidently sympatric with *M. sphagnicola*. It would be especially interesting to see mature fruits; if they are blue then red fruits are apomorphic for *M. sphagnicola*, while the discovery of red fruits would add to the similarities, likely synapomorphic, with *M. sphagnicola*.

3. Miconia sphagnicola Urb. & Ekman, Ark. Bot. 23A (11): 19. 1931.

TYPE: DOMINICAN REPUBLIC. Prov. Monte Cristi [now the border between Prov. Santiago and Prov. San Juan]: Monción, Cordillera Central, high ridge between Rio Cenobi and Rio San Juan, pine patch, ca. 1900 m, 11 Jun 1929 (fl), *E. L. Ekman H12808* (HOLOTYPE: S!; ISOTYPES: A!, GH!, IJ!, NY!, S!). Figure 3.

Low, often ± prostrate shrub to 0.4 m tall (but rarely to 1 m), and usually adventitiously rooting along prostrate portion of branches. Indumentum of multicellular, ferrugineous, irregularly stellate to globular-stellate hairs, and minute globular hairs. Young twigs ± rectangular in cross section, with two opposing faces slightly concave (i.e., those positioned above point of petiole attachment of adjacent proximal node) and the alternate faces slightly convex, 0.7–2 mm wide, becoming terete with age, the indumentum moderate to dense, multicellular, irregularly stellate to globular-stellate hairs, and minute globular hairs, with some elongate-branched hairs at the node, becoming only sparsely pubescent with age; internodes 2.5–13 (–23) mm long. Leaves with petiole 0.6–2 mm long, the indumentum ± sparse, similar to that of the twigs; blade ovate to elliptic, 4–13.3 × 2–5.75 mm, flat, coriaceous, the apex acute to obtuse, the base acute to rounded, the margin distinctly serrate, at least distally (ca. proximal 10–60% of margin entire), plane to revolute, the largest teeth to 0.1–0.9 mm, most narrowed to a slender apical portion having the form of a seta; venation acrodromous, basal, with prominent midvein and 1 pair of secondary veins, these placed 0.4–1 mm in from margin, and several percurrent tertiary veins oriented subperpendicular to midvein, the quaternary and higher-order veins obscure; adaxial surface green, not drying yellowish,

→

Figure 3. *Miconia sphagnicola*. A. habit; B. leaf, abaxial view; C. 4-merous flower; D. 5-merous flower; E. immature stamen; F. mature stamens, showing means of dehiscence; G. ovary and hypanthium in longitudinal section; H. ovary in cross section; J. stigma and distal part of style; K. berry; L. seed; M. hair. Originally published in Urban (1931).

J. Pohl del.

Miconia sphagnicola Urb. et Ekm.

the indumentum essentially glabrous, but occasionally with a few ferrugineous, ± stellate hairs on midvein, the midvein moderately to slightly impressed, the secondary veins slightly impressed or not impressed, the higher-order veins not impressed, surface wrinkled and minutely papillose after drying, in part because of the presence of scattered druse crystals; abaxial surface light green, moderately to sparsely covered with reddish brown minute globular hairs, with a few globular-stellate hairs on midvein and secondary veins, but these quickly deciduous, the midvein prominently to moderately raised, the secondary veins slightly raised to flat, all other veins flat. Inflorescences terminal, several-flowered, racemose to narrowly paniculate cymes of (0–) 1 to 3 major branch pairs, 1–4 (–5.2) cm long, 0.7–2.2 cm across; proximal segment of lowermost inflorescence branches (when present) 2.5–17 mm long, distal internodes increasingly shorter, ultimate branches 0–0.35 mm long, and flowers appearing in 3- (rarely 5-) flowered glomerules, terminating inflorescence and the inflorescence branches, but lateral dichasia reduced, each sometimes represented by a single flower, and even inflorescence branches sometimes reduced and bearing only a single, terminal flower (and inflorescence thus occasionally appearing to be a raceme, but with a terminal flower), with sparse hairs similar to those of twigs; peduncle 0.7–3 cm long, with similar indumentum; each inflorescence branch associated with ± deciduous, narrowly elliptic to obovate bract, 2–8.6 × 0.6–3 mm, the apex acute; flowers in dichasia, or seemingly solitary, each subtended by 2 caducous, narrowly elliptic, obovate, or linear bracteoles 0.95–2.5 × 0.2–0.8, the indumentum of a few minute globular hairs, the apices acute; the lowermost inflorescence branches sometimes in the axils of leaves. Flowers sessile or nearly so, the pedicel 0–0.25 mm long. Hypanthium cylindrical-orbicular, free portion 0.9–1.25 mm, the outer surface with scattered minute globular to minute and obscurely stellate hairs, the inner surface glabrous and not ridged or only indistinctly ridged. External calyx teeth 4 or 5, 0.2–0.75 × 0.4–0.9 mm, triangular, with ± acute apex, the indumentum glabrous or with a few minute globular hairs; internal calyx lobes 4 or 5, 0.38–0.7 × 0.8–1.05 mm, ovate-triangular, pale green to reddish, glabrous, the apex obtuse to rounded, the margin entire to minutely fimbriate; calyx tube 0.15–0.25 mm long. Petals 4 or 5, broadly elliptic to obovate, 1.7–3.6 × 1.2–2.1 mm, glabrous, white, imbricate and apically interlocking in bud, with apex rounded, with an asymmetrically located notch; margin entire. Stamens 8 or 10, geniculate; proximal portion 1.55–2.7 mm long; distal segment (anther and distal portion of filament) 2.05–3.05 mm long, the anther 1.25–1.65 mm long, with fertile

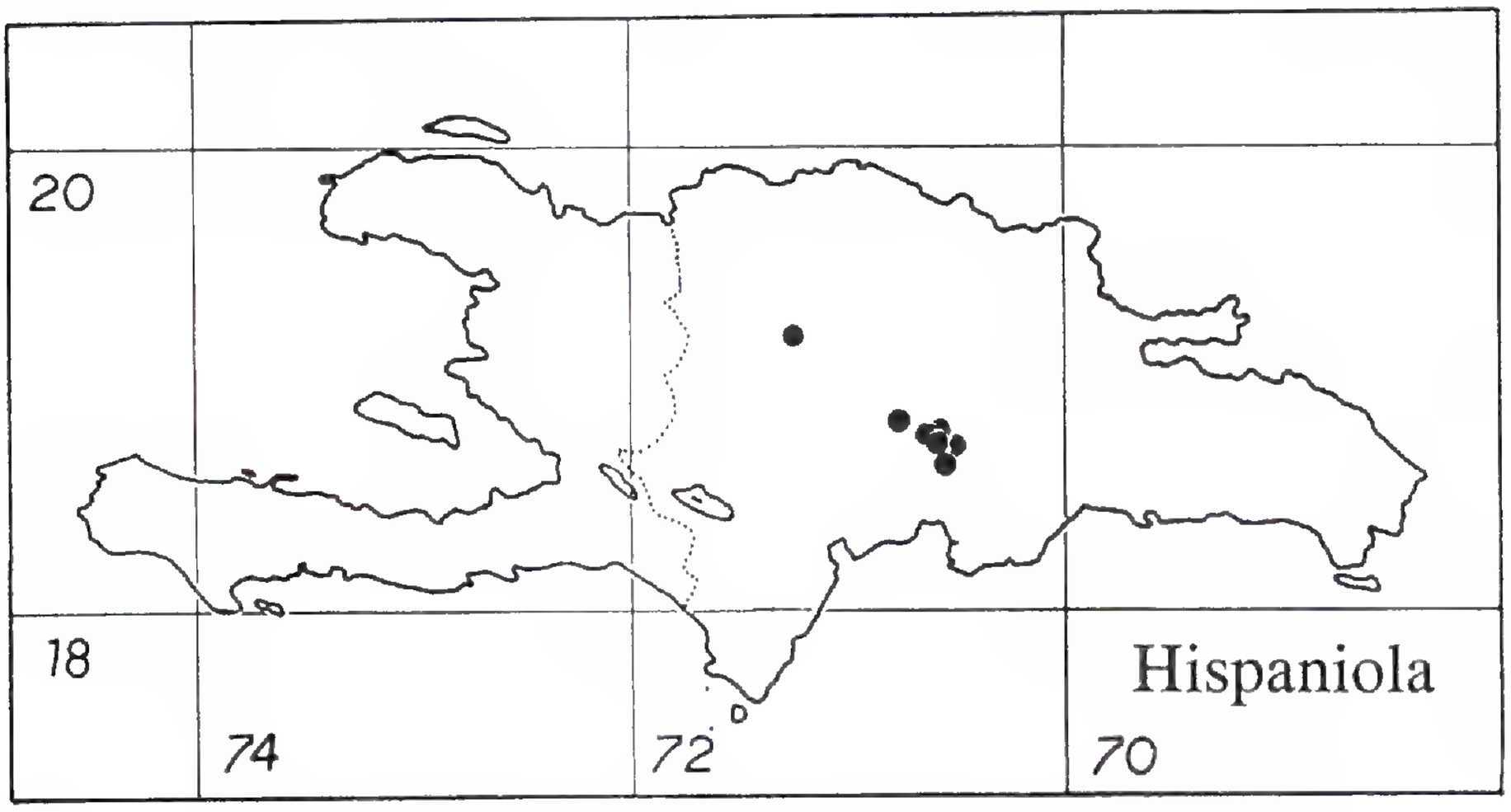

Figure 4. Distribution of *Miconia sphagnicola* on Hispaniola.

portion of anther sacs 0.9–1.35 mm long, opening by a single large, terminal pore, which extends, forming a short broadly to narrowly V-shaped longitudinal slit, with the septum between the anther sacs clearly visible, the base slightly lobed, and sometimes with a dorsal projection to ca. 0.1 mm long. Ovary 2- or 3-loculate (N = 6, 4), ca. inferior to ½-inferior, ± globose to ovoid, 0.6–1.3 × 0.5–1.2 mm, glabrous, not ridged or with variably developed ridges, and usually with minute, rounded apical projections, with crown 0.4–0.8 mm encircling the base of style; style 2.8–4.9 mm long; stigma usually slightly expanded. Berries globose to ellipsoid, 5.6–8.4 × 4–7.15 mm, bright red, essentially glabrous. Seeds rounded-pyramidal, 0.8–1.1 mm long; testa with isodiametric cells, minutely and densely tuberculate (due to bulging cells).

DISTRIBUTION AND ECOLOGY. *Miconia sphagnicola* is endemic to Hispaniola, where it occurs in the Dominican Republic, in the Cordillera Central (Figure 4), in cloud forests, grading into moist forests of *Pinus occidentalis*, or open, often burned forests of *P. occidentalis* with *Danthonia domingensis* Hack. & Pilg. and various shrubby species [e.g., *Baccharis myrsinites*, *Eupatorium illitum*, *Fuchsia pringsheimii* Urb., *Garrya fadyenii*, *Myrica picardae*, *Ilex tuerckheimii* Loes., *Miconia viscidula* Urb. & Ekman, *Lyonia heptamera* Urb., *L. tuerckheimii* Urb., *L. urbaniana* (Sleumer) J. Jiménez Alm.], from 1900–2400 m (see also Hager and Zanoni 1993; Horn et al. 2001). Associated melastomes include *Miconia selleana*, *M. viscidula*, *M. krugii* Cogn., *M. monciona*, and *Tetrazygia urbaniana*.

SPECIMENS EXAMINED: DOMINICAN REPUBLIC. Prov. La Vega: Valle Nuevo, 2400 m, *Bro. Augusto 1497* (A, JBSD, NY); 5 km above La Nuez on rd. to Constanza, *W. G. D'Arcy 2662* (FLAS, MO); Cordillera Central, Loma la Chorriosa, 18°46′N, 70°35′W, 2270 m, *R. García 5764* (FLAS); Cordillera Central, ca. 2 km N of "The Monument," Valle Nuevo, on rd. between Constanza and San José de Ocoa, ca. 34.6 km S of Constanza, 2200 m, *W. S. Judd 5115* (A, DUKE, FLAS, MO, NY, S, US); La Nevera, from Valle Nuevo to San José de Ocoa, 2100 m, *A. H. Liogier 13154* (F, GH, NY); La Nevera, Valle Nuevo, 2100 m, *A. H. Liogier 20676* (JBSD, NY); Valle Nuevo, Constanza, 2100 m, *A. H. Liogier 22354* (JBSD); Cordillera Central, along Rt. 41, ca. 2 km N of the monument at Valle Nuevo, 34.6 km S of Constanza, 2200 m, *J. D. Skean 1739* (FLAS); Cordillera Central, 5.4 km S of Constanza, and between 6 and 8 km W on rd. to Pinar Parejo, 18°50′N, 70°45′W, 6200–6300 ft., *T. A. Zanoni 19346* (FLAS, JBSD, NY); Cordillera Central, 39 km S of Constanza via the village of Río Grande, on the rd. to San José de Ocoa, "The Pyramid" monument, in the Arroyo Domingo, 18°49′N, 70°42′W, 7500 ft., *T. A. Zanoni 20130* (FLAS, JBSD, NY); Cordillera Central, Loma de Mono Mojao and Arroyo Las Piedras, 36 km S of Constanza and 2 km E of the rd., 18°43′N, 70°35′W, 7000 ft., *T. A. Zanoni 20874* (FLAS, JBSD); Cordillera Central, 45.5 km N of San José de Ocoa, 2 km N of "The Pyramid," a monument, on rd. to Constanza, 18°42.5′N, 70°36′W, 2280 m, *T. A. Zanoni 29099* (FLAS, JBSD, NY).

When this very distinctive species was described, Urban and Ekman (Urban 1931) considered it to be not closely related to any other Antillean species of *Miconia*. This statement is puzzling given the noteworthy morphological similarities with *M. monciona*, such as the small leaves and low stature. We note that *M. monciona* was described in the same publication as *M. sphagnicola* (Urban 1931) and that E. Ekman had collected these two species growing together in a high-elevation pineland.

Miconia sphagnicola is unique among Hispaniolan species of *Miconia* in its more or less prostrate habit, with frequent production of adventitious roots along the branches. The species is also distinctive because of its minute leaves (i.e., 4–13.3 mm long) with only a single pair of secondary veins, and the ellipsoid, red berries. Most species of *Miconia* have two or more pairs of secondary veins, and no other Hispaniolan species has red fruits (most have blue, blue-black, or purple fruits, at least at maturity).

4. Miconia tetrastoma Naudin, Ann. Sci. Nat., Bot., sér. 3, 16: 236. 1851. TYPE: CUBA. Prov. Oriente. Sierra Maestra, *J. J. Linden 2002* (HOLOTYPE: presumably at BR, not seen). Figure 5.

Shrub to 6 m tall. Indumentum of multicellular, ferrugineous to whitish, roughened-granular, sessile to stalked, globular-stellate to dendritic, or elongate-branched hairs, often matted and disintegrating

Figure 5. *Miconia tetrastoma*, flowering, from Morne Formon, Massif de la Hotte, Haiti.

with age, and minute globular hairs. Young twigs rectangular in cross section, with two opposing faces slightly concave (i.e., those positioned above point of petiole attachment of adjacent proximal node) and the alternate faces slightly convex, 1–3.5 mm wide, becoming ± quadrangular with age, the indumentum of moderate to sparse multicellular, elongate-branched, irregularly stellate, dendritic, to globular stellate hairs, these roughened-granular (due to bulging to papillae-like, thin-walled cells), and minute globular hairs, the hairs often becoming matted and disintegrating, and stems only sparsely pubescent with age; internodes 1–5.7 cm long. Leaves slightly anisophyllous, with petiole 6–18 mm long, the indumentum very sparse to moderate, similar to that of twigs; blade broadly to narrowly elliptic, or slightly ovate, or obovate, 3.4–14.5 × 1.7–6.2 cm, flat to V-shaped, membranous to slightly coriaceous, the apex acuminate to long-acuminate, rarely acute, the base acute, obtuse, to rounded, the margin distinctly serrate, nearly throughout (ca. proximal 0–10% of margin entire), plane, the largest teeth to 0.3–0.97 mm, most narrowed to a slender apical portion having the form of a seta; venation acrodromous, basal to suprabasal, with prominent midvein and 2 pairs of secondary veins, with 1 pair of conspicuous secondary veins placed 3–14 mm in from margin and a second pair of inconspicuous secondary veins placed 0.5–2.4 mm in from margin, these

often ± intramarginal, and rarely with an additional, partial, intramarginal outermost pair of veins, but these disappearing toward leaf base (or becoming composed on obviously inter-linked tertiary veins), and numerous percurrent tertiary veins oriented subperpendicular to midvein, the tertiary veins usually connected by quaternary veins but sometimes separated by variously developed composite-intertertiary veins; adaxial surface green, the indumentum essentially lacking, but with some ferrugineous to whitish, ± stellate to dendritic, roughened and often disintegrating hairs along midvein and major secondary veins, and with minute globular to short-armed hairs even on lamina, but these deciduous with age, the midvein through quaternary veins flat to moderately impressed, the surface minutely wrinkled when dry, with scattered minute "papillae" due to presence of druse crystals; abaxial surface light green, moderately to very sparsely covered with minute globular hairs, with a few to numerous roughened and often disintegrating, ± obscurely stellate to dendritic hairs on midvein and secondary veins, but these often deciduous, the midvein and secondary veins prominently to slightly raised, tertiary and quaternary veins slightly raised to flat, all other veins ± flat; sometimes with pouch-domatia at junction of major secondary veins and midvein. Inflorescences terminal, many-flowered, paniculate to racemose cymes of 3 to 8 major branch pairs, 2.5–8 cm long, 1.6–6.7 cm across; proximal segment of lowermost inflorescence branches 0.4–3 cm long, distal internodes increasingly shorter, ultimate branches 0.8–1.7 mm, and flowers not in glomerules, with sparse to moderate hairs similar to those of the twigs; peduncle 1.1–3 (–6) cm long, with similar indumentum; each inflorescence branch associated with deciduous, narrowly elliptic to obovate bract, 2–7.3 × 0.5–2.5 mm, the apex acute; flowers in dichasia, each subtended by 2 caducous, ± narrowly elliptic, ± linear, or narrowly obovate bracteoles 1–3 × 0.3–0.65 mm, the indumentum of irregularly branched hairs along margin, the apex acute to acuminate; the lowermost inflorescence branches sometimes in the axils of leaves. Flowers nearly sessile to distinctly pedicellate, the pedicel 0.15–0.65 mm long. Hypanthium cylindrical-orbicular, free portion 0.5–1.12 mm long, the outer surface with ± sparse, ferrugineous, minute globular to irregularly short-branched hairs, the inner surface with scattered minute globular hairs, especially toward rim, slightly ridged, due to extensions of partitions dividing lower portion of space between hypanthium and gynoecium into 10 pockets, into which fit the anthers (when reflexed, in bud). External calyx teeth 5, 0.15–0.4 × 0.8–1.4 mm, triangular, with acuminate apex, ± glabrous; internal calyx lobes 5, 0.3–0.4 × 0.8–1.4 mm, triangular, pale green, glabrous, the apex obtuse to

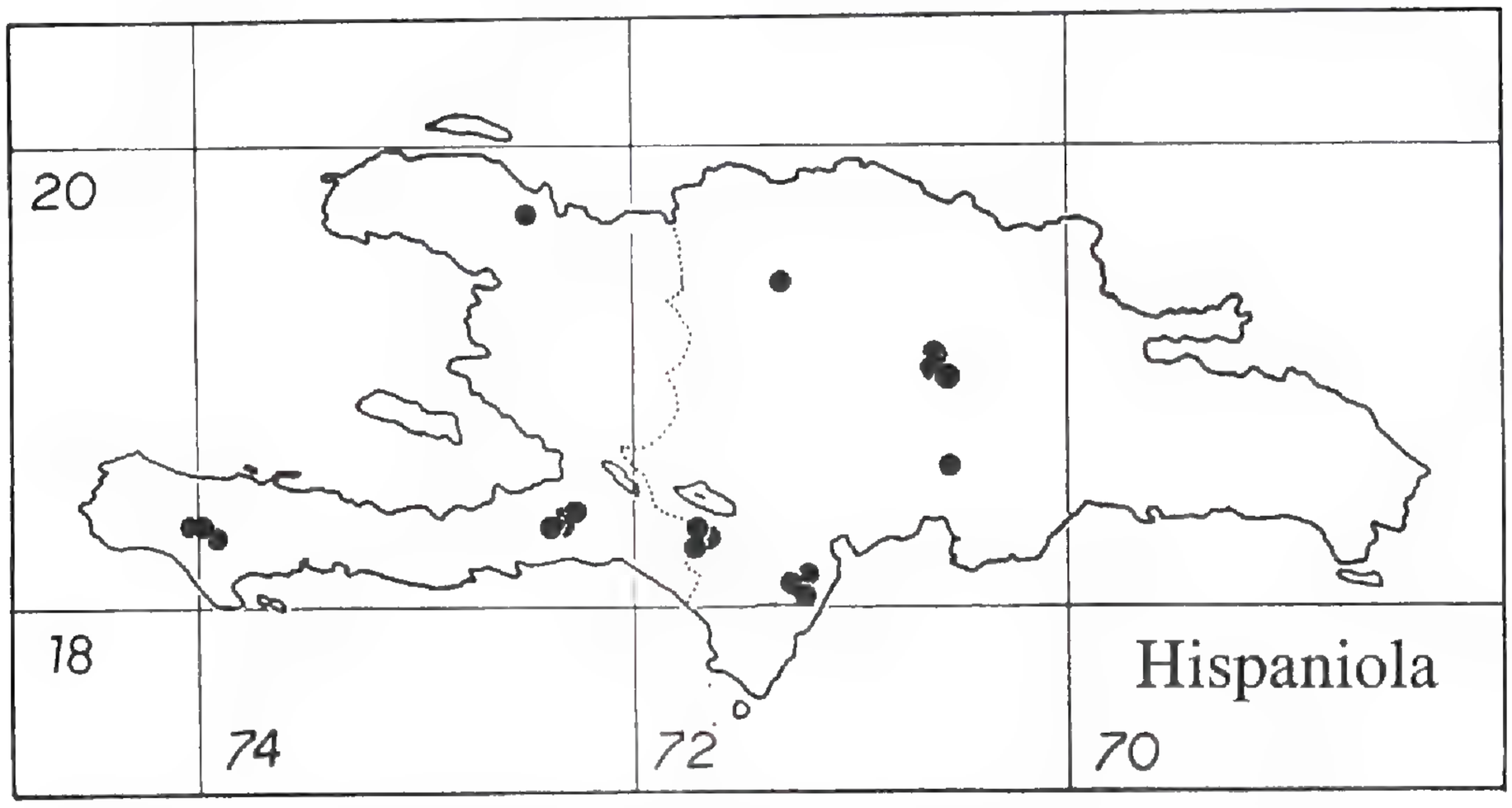

Figure 6. Distribution of *Miconia tetrastoma* on Hispaniola.

rounded or truncate, the margin entire to minutely erose; calyx tube 0.1–0.47 mm long. Petals 5, ± broadly elliptic, 1.75–2.45 × 1.45–1.75 mm, glabrous, white, imbricate and apically interlocking in bud, with apex rounded, with an asymmetrically located notch; margin entire. Stamens 10, geniculate; proximal portion 1.5–1.85 mm long; distal segment (anther and distal portion of filament) 1.8–2.4 mm long, the anther 1.25–1.6 mm long, with fertile portion of anther sacs 0.7–1.05 mm long, opening by a single, large, ventrally inclined, terminal pore, with the septum between the anther sacs clearly visible, extending beyond the pore apex, four-parted, dividing the pore into 4 smaller pores, the base tapering to filament, and with a slightly to strongly dorsally thickened (to 0.2 mm) connective. Ovary 3-loculate (N = 9), inferior or nearly so, ± globose, 1.05–1.7 × 1–1.35 mm, with a few minute globular hairs, especially near apex, strongly ridged, and these ending in minute, rounded apical projections, with crown to 0.25–0.7 mm encircling the base of style; style 2.8–3.6 mm long; stigma somewhat expanded. Berries globose, 3–6 × 3–6 mm, pale to deep blue or blue-black, glabrous. Seeds ± hemispherical to asymmetrically hemispherical, 0.4–0.55 mm long, with a broad and flat raphe; testa with isodiametric cells, minutely and densely tuberculate (due to bulging cells).

DISTRIBUTION AND ECOLOGY. *Miconia tetrastoma* is restricted to Cuba, where it occurs in the Sierra Maestra (Leon and Alain 1957), and Hispaniola, where it occurs in the Cordillera Central/Massif du Nord, Massif de la Selle/Sierra de Baoruco, and Massif de la Hotte (Figure 6), in cloud forests and moist montane forests, moist forest on limestone, and

moist forests of *Pinus occidentalis*, from (800–) 1100–2219 m. Associated species of Melastomataceae include *Calycogonium torbecianum* Urb. & Ekman, *Clidemia umbellata* (Mill.) L. O. Williams, *Conostegia affinis* Urb., *C. icosandra* (Sw.) Urb., *Henriettea barkeri* (Urb. & Ekman) Alain, *Leandra lima* (Desr.) Judd & Skean, *L. limoides* (Urb.) Judd & Skean, *Mecranium amygdalinum* (Desr.) C. Wright *in* Sauvalle, *M. birimosum* (Naudin) Triana, *M. multiflorum* (Desr.) Triana, *M. ovatum* Cogn., *M. puberulum* Cogn., *M. revolutum* Skean & Judd, *Meriania brevipedunculata* Judd & Skean, *M. involucrata* (Desr.) Naudin, *M. parvifolia* Judd & Skean, *Miconia barkeri* Urb. & Ekman, *M. dielsiana* Urb., *M. domingensis* Cogn., *M. favosa* (Desr.) Naudin, *M. howardiana* Judd, V. T. Salzman & Skean, *M. hypiodes* Urb. & Ekman, *M. lanceolata* (Desr.) DC., *M. mirabilis* (Aubl.) L. O. Williams, *M. punctata* (Desr.) D. Don, *M. subcompressa* Urb., *M. xenotricha* Urb. & Ekman, *Sagraea curvipila* (Urb. & Ekman) Alain, *S. oligantha* (Urb.) Alain, *S. scalpta* (Vent.) Naudin, and *Tetrazygia crotonifolia* (Desr.) DC. Moist forest associates are very diverse; for a listing of characteristic species of the forests of the Massif de la Hotte see Judd (1987) and Judd et al. (1990, 1998), for the forests of Barbacoa-Casabito region see Mejía et al. (2000) and García et al. (1994), and for a general analysis of the vegetation of Hispaniola see Hager and Zanoni (1993) and Ciferri (1936).

SPECIMENS EXAMINED: DOMINICAN REPUBLIC. Prov. Barahona: La Tierra Fria, SW of Barahona, 4600 ft., *R. A. Howard 12223* (A, S, US); between Monteada Nueva and Loma Alta, 5000 ft., *R. A. Howard 12325* (A, S, US); Sierra de Baoruco, Monteada Nueva, near Polo, 1400–1425 m, *W. S. Judd 5179* (FLAS, JBSD, NY, S); Sierra de Baoruco, Monteada Nueva, above Polo, 1325–1400 m, *W. S. Judd 6578* (FLAS); Monteada Nueva, "Caña Brava," S of Cabral, 1300 m, *A. H. Liogier 11639* (NY, US); Caña Brava, Monteada Nueva, Barahona, 1300 m, *A. H. Liogier 25145* (GH, JBSD, NY); Monteada Nueva, *E. Marcano* [*Herb. J. Jiménez* No.] *5281* (NY); Sierra de Baoruco, Loma "Pie Pol" (Pie de Palo) de La Guasára de Barahona, 18°10′N, 71°12′W, 1250 m, *T. A. Zanoni 38645* (FLAS); Sierra de Baoruco, Loma Pie de Pol (Pie Pol), 18°10′N, 71°13′W, 1400 m, *T. A. Zanoni 41116* (FLAS). Prov. Independencia: Zapotén, El Aguacate, Duvergé, 1300 m, *A. H. Liogier 27014* (JBSD, NY); Sierra de Baoruco, 38 km S of Duvergé, or 5 km S of Aguacate, along the International Highway between Los Arroyos and Pedernales, 18°18′N, 71°42.5′W, 1550–1600 m, *T. A. Zanoni 26569* (FLAS). Prov. Monseñor Nouel: rd. to Alto Casabito, ca. 8 km from junction with Highway Duarte, 890–925 m, *W. S. Judd 6525* (FLAS). Prov. Pedernales: above Los Arroyos, 1700 m, *A. H. Liogier 23221* (JBSD, NY). Prov. Peravia: Cordillera Central, 15 km N of Parque Central de San José de Ocoa and 10 km from the "cruce de Los Arroyos" on rd. to Carmona, 18°40′N, 70°32′W, 4400 ft., *T. A. Zanoni 21449* (FLAS). Prov. Santiago Rodriguez: Cordillera Central, Monción, Lagunas de Cenobi, ca. 1100 m, *E. L. Ekman H12765* (A, GH, S, US). Prov. La Vega: Cordillera Central, Reserva Científica Ebano Verde, Loma Golondrina, 1400–1565 m, 19°30′N, 70°33′W, *R. García 46123* (FLAS); Cordillera

Central, Loma La Golondrina, ca. 1565–1500 m, E from Paso Bajito, *W. S. Judd 5159* (FLAS, GH, JBSD); Loma de la Sal, Jarabacoa, 1200 m, *A. H. Liogier 11367* (NY, US); Loma de la Sal, Jarabacoa, 1000–1400 m, *A. H. Liogier 11945* (GH, US); Loma de la Sal, Jarabacoa, 1300–1400 m, *A. H. Liogier 13389* (GH, US); Alto Casabito, Bonao, 1300 m, *A. H. Liogier 18308* (F, NY); Alto Casabito, Bonao, 1300 m, *A. H. Liogier 23006* (JBSD, NY); Loma de la Sal, Jarabacoa, 1200 m, *A. H. Liogier 23613* (JBSD, NY); Cordillera Central, Loma La Golondrina, 1525 m, *J. D. Skean 1786* (FLAS).

HAITI. Dept de L'Ouest: Massif de la Selle, Furcy, 1540 m, *E. L. Ekman H1290* (S); Massif de la Selle, Parc National Morne la Visite, Morne d'Enfer, 1850–1880 m, *W. S. Judd 4662* (EHH, FLAS); Parc National Morne la Viste, between Morne d'Enfer and Morne Fe Noir, 1660–1735 m, *W. S. Judd 4763* (FLAS); Massif de la Selle, along Kenscoff Rd. 2.9 mi. S of junction with rd. to Morne Teleco (= Morne Tranchant), ca. 5.4 mi. S of Kenscoff and 0.3 mi. N of Furcy, 1560 m, *W. S. Judd 6822* (EHH, FLAS). Dept. du Nord: Massif du Nord, Port Margot, top of Morne Maleuvre, ca. 1150 m, *E. L. Ekman H2815* (S, US). Dept. du Sud: mountains of "La Hotte," near Aux Cayes, ca. 800 m, *E. L. Ekman H142* (NY, S); Morne de la Hotte, western slopes of "Ma Blanche," ca. 1400 m, *E. L. Ekman H549* (NY, S); Massif de la Hotte, Parc National Pic Macaya, Morne Formon, ridge and N slopes, 1650–1800 m, *W. S. Judd 3741* (EHH, FLAS); Parc National Pic Macaya, Morne Cavalier, ca. 1530–1560 m, *W. S. Judd 4025* (FLAS, JBSD); Parc National Pic Macaya, S slopes of Morne Formon, just E of Pic Le Ciel, 1850–1950 m, *W. S. Judd 5742* (FLAS); Parc National Pic Macaya, near Deron plain, Bwa Deron, 1150–1190 m, *W. S. Judd 6904* (EHH, FLAS); Massif de la Hotte, Macaya Biosphere Reserve, S slopes of Morne Formon, in Ravine Fond Bleu, 1275–1300 m, *W. S. Judd 5759* (FLAS); Macaya Biosphere Reserve, Ravine de Sud, Gran Ravine, N slopes of Morne Formon, 1450–1780 m, *J. D. Skean 1346* (EHH, FLAS); *ibid.*, *J. D. Skean 1379* (EHH, FLAS); Macaya Biosphere Reserve, along high ridge from Morne Macaya to Pic Formon and Pic le Ciel, 1900–2219 m, *J. D. Skean 1470* (FLAS); Macaya Biosphere Reserve, ridge of Morne Formon, 1830–1860 m, *J. D. Skean 1538* (FLAS); Massif de la Hotte, Morne Formon, on the ridge, 1820 m, *J. D. Skean 1677* (DUKE, EHH, FLAS); Massif de la Hotte, Macaya Biosphere Reserve, Morne Formon, ridge E of Pic le Ciel, 1900–2100 m, *J. D. Skean 2449* (FLAS).

Miconia tetrastoma is phenetically distinctive because of its unusual branched hairs on the stems, inflorescence axes, and leaves, which have a distinctive granular surface texture due to the presence of numerous bulging, thin-walled cells. The species also has distinctive 4-pored anthers, and its flowers are not in dense glomerules. The leaves are immediately separable from other species of section *Cremanium* on Hispaniola because of acuminate to long-acuminate apices.

Miconia tetrastoma occurs at lower elevations, in a wider variety of habitats, and is more widespread (Figure 6) than any other species of section *Cremanium* on Hispaniola.

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A FLORISTIC SURVEY OF THE FORESTED PARTS OF THE UNITED PLANT SAVERS' ETHNOBOTANICAL SANCTUARY, MEIGS COUNTY, OHIO

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ABSTRACT. The United Plant Savers' (UpS) botanical sanctuary in southeastern Ohio was created to protect native medicinal plants by protecting their habitat. Located in the southern unglaciated Allegheny Plateau physiographic province, this 155 ha preserve is 70% (110 ha) deciduous forest, 30% (45 ha) old fields, and contains one small opening that was surveyed to determine whether it was a remnant prairie. A floristic survey of the vascular plants of the wooded portions of the sanctuary and the opening revealed 358 species in 238 genera and 97 families. This total includes two state-listed, "potentially threatened" species: *Corallorhiza wisteriana* and *Juglans cinerea*. Nine percent of the species identified are non-native to southeastern Ohio. The vegetation found in the opening does not indicate that it is actually a prairie.

Key Words: vascular flora, Ohio, botanical sanctuary, conservation, medicinal plants, United Plant Savers

The United Plant Savers (UpS), a non-profit organization working in the United States and Canada, promotes the conservation of native medicinal plants and their habitat through education and land preservation. Their land preservation effort is primarily carried out through a botanical sanctuary network in which UpS members can designate private land for in-situ conservation of medicinal plants. Their education programs focus on community workshops and summer internships. In Meigs County, Ohio, the UpS established their largest sanctuary, a 155 ha preserve of forest and field, in 1999.

Study site. The Meigs County sanctuary (39°5′N, 82°9′W, Rutland Quadrangle; United States Geological Survey 1995) is in southeastern Ohio, approximately 20 miles south of Athens (Figure 1). The sanctuary is located in southwestern Meigs County, in Rutland Township. Covering 155 ha, it is composed of 70% secondary forest and 30% old fields. There is also one small opening located on a hilltop in the southwestern portion

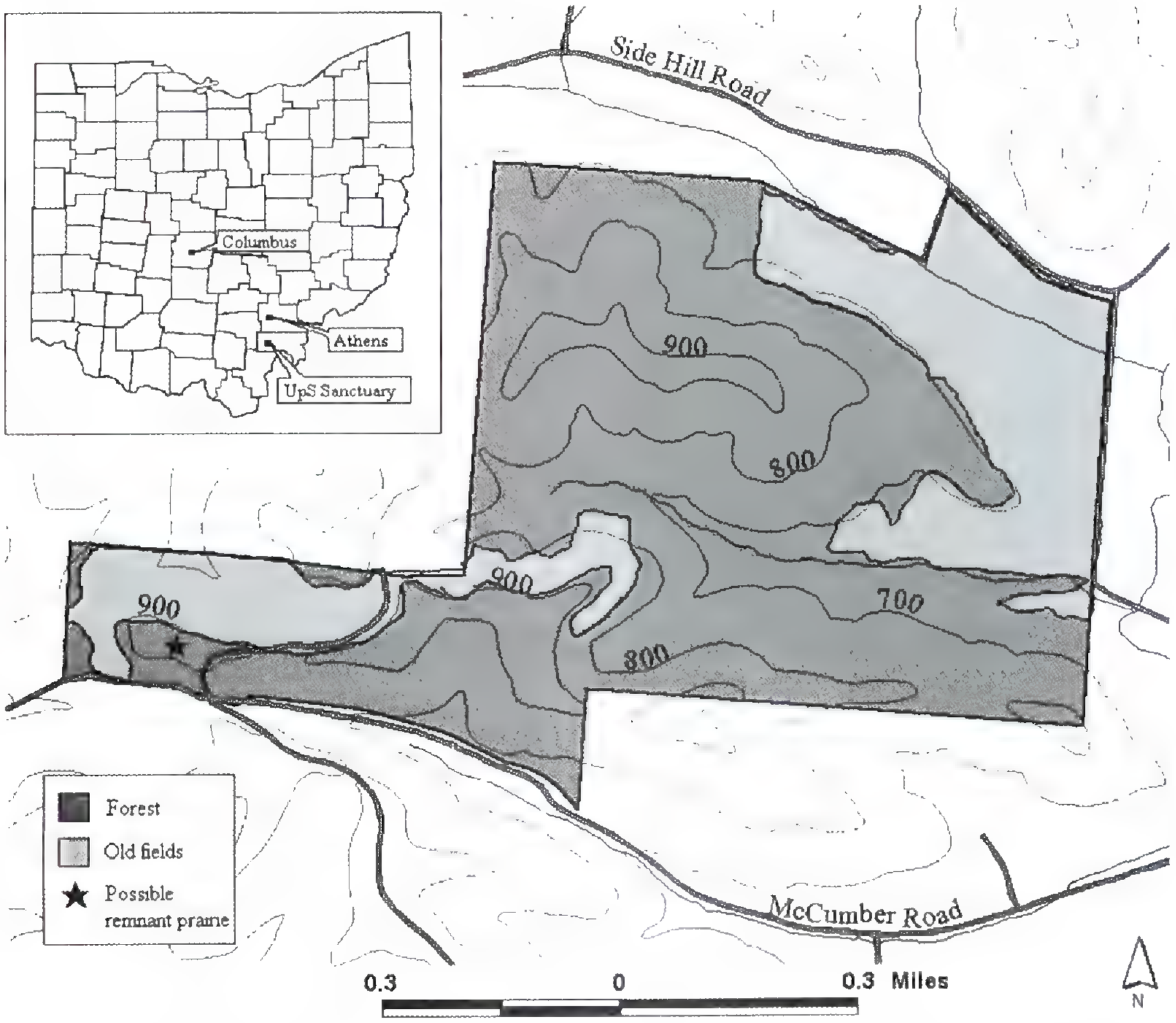

Figure 1. Location of the United Plant Savers' sanctuary in Meigs County, Ohio. Sanctuary land is outlined in black. The dark shaded regions represent the forested portions of the sanctuary. The light shaded regions represent the old fields, including the one converted to the planted prairie, that were not surveyed in this study.

of the sanctuary, which was considered a possible remnant prairie. This opening plus the wooded portion constitute about 110 ha of the sanctuary.

Climate. Climate in southeastern Ohio is temperate, with hot summers and cold winters. Precipitation falls year round. Temperature and precipitation data for Carpenter, Ohio (39°9′N, 82°17′W) are provided in Table 1. Mean annual snowfall in Meigs County is 53.3 cm (Gilmore and Bottrell 1999).

Physiography and geology. Meigs County is part of the southern unglaciated Allegheny Plateau, which makes up a portion of the larger Appalachian Plateau physiographic province (Braun 1961). This high-relief area is composed of narrow ridgetops (which run primarily in an east-west direction), hills, and stream valleys (Gilmore and Bottrell 1999). Within the sanctuary, elevation ranges from 190 to 280 meters

Table 1. Temperature and precipitation data collected from Carpenter, Ohio in Meigs County (National Climatic Data Center and National Oceanic and Atmospheric Association 2001).

	Annual	Minimum (Month)	Maximum (Month)
Mean temperature (°C)	11.3	−1.6 (Jan)	22.8 (Jul)
Mean temperature 2000 (°C)	11.1	−4.8 (Dec)	21.3 (Aug)
Mean temperature 2001 (°C)	11.8	−1.7 (Jan)	23.1 (Aug)
Mean precipitation (cm)	104.33	6.49 (Oct)	11.27 (May)
Precipitation 2000 (cm)	90.65	2.11 (Oct)	16.10 (Feb)
Precipitation 2001 (cm)	93.27	3.96 (Sep)	18.52 (May)

(United States Geological Survey 1995). The bedrock underlying the sanctuary is sandstone and shale from the Monongahela and Conemaugh groups of the Pennsylvanian system with outcroppings from the Ames limestone interval (Schumacher 1995).

Soils. The majority of the soils on slopes and ridgetops in the sanctuary are Alfisols and Ultisols, specifically Upshur (fine, mixed, mesic Typic Hapludalfs) – Gilphin (fine-loamy, mixed, mesic Typic Hapludults) complexes (Gilmore and Bottrell 1999). On slopes, these are deep to moderately deep, well-drained soils with a silt loam surface layer. The Upshur subsoil is silty clay loam and silty clay, and the Gilphin subsoil is channery loam, very channery loam, and silt loam. On ridgetops the soils are deep to very deep and well-drained. The surface silt-loam layer has been partially eroded. The Upshur subsoil is silty clay loam and silty clay, and the Gilphin subsoil is silt loam and silty clay loam. Soils in areas that have been strip-mined in the past are Entisols. These are very deep, excessively well-drained, Pinegrove (mixed, mesic Typic Udipsamments) coarse sand loams. Intermittent stream bottoms have Inceptisols from the Chagrin (fine-loamy, mixed, mesic Dystric Fluventic Eutrochrepts) series. These soils are very deep, well-drained silt loams that are frequently flooded (Gilmore and Bottrell 1999).

Vegetation. Delcourt and Delcourt (1988) described this region as eastern deciduous forest. This forest type has characteristic multistoried vegetation, a diverse understory, and a rich flora of spring ephemerals. Within the preserve, the ridges and upper slopes support oak-hickory forest, whereas mixed mesophytic forest predominates on lower slopes and stream terraces. Mixed mesophytic forest (Braun 1950) is a general term describing deciduous forest with multiple canopy codominants, including *Acer saccharum*, *Aesculus flava*, *Fagus grandifolia*,

Liriodendron tulipifera, *Quercus alba*, *Q. rubra*, *Tilia americana*, and formerly *Castanea dentata*.

Land use. The major industry in Meigs County, both in the past and today, has been agriculture. Other natural resource industries present in the county are the extraction of coal, oil, gas, timber, sand, and gravel (Gilmore and Bottrell 1999). Historically, the sanctuary land has been farmed, grazed, logged, and strip-mined for coal (Zanski 1997). There are several old fields in the sanctuary that mark past agricultural use and were not included in this study. Other areas on the sanctuary represent past strip-mining operations. These areas are now characterized by open fields at the base of steep, sandstone rock walls that were created by the mining process.

Since the early 1970s, natural vegetation on what is now the sanctuary has been regenerating. Current restoration and reconstruction efforts in the UpS sanctuary have centered on two ecosystem types—forest and prairie. Within the forest, there has been mostly natural regeneration. Only two species that were not found there previously, *Cypripedium parviflorum* and *Chamaelirium luteum*, have been purposely introduced. Additionally, *Panax quinquefolius*, *Hydrastis canadensis*, and *Cimicifuga racemosa* populations, which were already present when the preserve was created, have been expanded by spreading seed within the forest (Paul Strauss, UpS, pers. comm.). The conversion of an old field to a planted prairie has involved more habitat manipulation with the introduction of species that are native to western Ohio prairies. There is, though, one opening (the possible remnant prairie) that has not been intentionally altered by the preserve managers (Paul Strauss, UpS, pers. comm.). Although much of the land in Meigs County is used for farming or natural resource extraction, the sanctuary is surrounded by 1700 acres of private, mostly forested land managed with a similar conservation philosophy.

Objectives. The flora of the UpS sanctuary has never been systematically recorded. This study provides baseline data on the vascular flora of the wooded portion of the sanctuary and the possible remnant prairie, in order to facilitate future research on the sustainability and population ecology of medicinal plants.

MATERIALS AND METHODS

The vascular flora was surveyed on the UpS land from May through October 2000 and from March through October 2001. During both

Table 2. Description of abundance ratings as developed by Palmer et al. (1995).

Density	Score	Description
Abundant	5	Dominant or codominant in one or more common habitats
Frequent	4	Easily found in one or more common habitats but not dominant in any common habitat
Occasional	3	Widely scattered but not difficult to find
Infrequent	2	Difficult to find with few individuals or colonies, but found in several locations
Rare	1	Very difficult to find, limited to one or very few locations/uncommon habitats

years, biweekly trips were made to the sanctuary. Random paths were walked through the 110 ha study area in order to cover it as thoroughly as possible. All forested areas, forest edges, and the possible remnant prairie site were surveyed. The planted prairie and the fields were excluded from the study. Two voucher specimens were made for each species: one for the Bartley Herbarium at Ohio University (BHO) and one for the UpS collection.

To organize the floristic survey, the study area was divided into units following topographic boundaries. These included ridgetops, slopes, and stream terraces. Each unit was surveyed several times during the year to document the flora. For each species found, general habitat was noted (i.e., whether it occurred along the stream terraces, on the slopes, on ridgetops, in the possible remnant prairie, or in some combination of these areas). Additionally, an abundance score from one to five was determined for each species based on a scale developed by Palmer et al. (1995; Table 2). For this study, a score of 5 was used only for woody species, whereas all other scores were used for both woody and herbaceous species.

Species were identified using Braun (1961, 1967), Cooperrider (1995), Fisher (1988), Gleason and Cronquist (1991), and Holmgren (1998). Nomenclature, family classification, and native/non-native species status follow Cooperrider et al. (2001), with the following exceptions. *Phryma* is assigned to Phrymaceae rather than Verbenaceae, based on recent molecular evidence that it is not closely related to Verbenaceae (Beardsley and Olmstead 2002). Retaining a broader

Table 3. Number of taxa found in forested portions and possible remnant prairie of United Plant Savers' sanctuary, Meigs County, Ohio.

			Species		
Division	Families	Genera	Native	Non-native	Total
Lycopodiophyta	1	1	1	0	1
Polypodiophyta	7	14	19	0	19
Pinophyta	2	2	2	0	2
Magnoliophyta	87	221	303	33	336
TOTAL	97	238	325	33	358

circumscription of *Eupatorium* (Gleason and Cronquist 1991), *E. rugosum* is not treated as *Ageratina*, as in Cooperrider et al. (2001).

RESULTS

A total of 358 species in 238 genera, 97 families, and four divisions of vascular plants were identified from the forest and possible remnant prairie combined (Table 3; Appendix). Approximately 9% (33) of the species in the total flora were not native to southeastern Ohio. Within the wooded portions of the sanctuary, 331 species were identified, about 8% (26) of which were non-native (Table 4). In the possible remnant prairie, there were 84 species identified, about 15% (13) of which were non-native (Appendix).

For the entire flora, the families with the most species were Asteraceae (37 species), Poaceae (24), Lamiaceae (18), Rosaceae (18), Cyperaceae (16), and Fabaceae (15). Genera with the most species were *Carex* (14 species), *Aster* (7), *Desmodium* (7), *Galium* (5), *Hypericum* (5), *Polygonum* (5), and *Solidago* (5). Thirty-three species in 20 families were non-native to southeastern Ohio. The families with the most non-native species were Asteraceae (4 species), Poaceae (4), Brassicaceae (3), and Fabaceae (3).

Of the 33 non-native species, 16 were found solely in forest edge habitats or the possible remnant prairie. Of these 16, *Ailanthus altissima* and *Melilotus officinalis* are listed among the most invasive plants in Ohio, and *Daucus carota* is listed as a well-established non-native species [Ohio Department of Natural Areas and Preserves (ODNAP) 2000] and as a noxious weed (Rose and Sheaffer 1998). Of the 17 non-native species found in the interior of the forest, three are considered among Ohio's most invasive plants (*Elaeagnus umbellata*, *Lonicera japonica*, and *Rosa multiflora*). Additionally, *Berberis thunbergii* is listed as a well-established non-native species (ODNAP 2000), and

Table 4. Floristic data from regional and smaller-scale floras of the unglaciated Appalachian Plateau: unglaciated Ohio (Cusick and Silberhorn 1977), The Ridges (Kline 1994), Dysart Woods (Johnson 2001), and Lilley Cornett Woods (Sole et al. 1983). All smaller-scale floras represent forest only. The size of unglaciated Ohio is an estimated value.

	Size (ha)	Number of		Percent Non-native Species
		Species	Families	
United Plant Savers, Ohio (total)	110	358	97	9
Unglaciated Ohio	3,200,000	2029	141	24
United Plant Savers, Ohio (forest)	110	331	95	8
The Ridges, Ohio	95	295	94	17
Dysart Woods, Ohio	35	233	69	18
Lilley Cornett Woods, Kentucky	105	304	78	–

Chrysanthemum leucanthemum is included in the state noxious weed list (Rose and Sheaffer 1998). It is noteworthy that several species that are invasive in southern Ohio forests were not found at the sanctuary (including *Alliaria petiolata*, *Celastrus orbiculatus*, *Euonymus alatus*, *E. fortunei*, *Ligustrum vulgare*, and *Lonicera maackii*).

Two species from the flora are state-listed as "potentially threatened:" *Juglans cinerea* and *Corallorhiza wisteriana* (ODNAP 2002). Five species are considered characteristic of southeastern Ohio (Cusick and Silberhorn 1977). These species are typical of the southern Appalachians, and in Ohio they reach the northern limit of their range on the southern Allegheny Plateau. They are *Aesculus flava*, *Elephantopus carolinianus*, *Oxydendrum arboreum*, *Salvia lyrata*, and *Scutellaria serrata*.

DISCUSSION

Comparison with other floras. The total UpS sanctuary flora (forest and possible remnant prairie) was compared with the regional flora of unglaciated Ohio, and the forest flora of the UpS was compared with several smaller-scale forest floras (Table 4). As of 1977 (Cusick and Silberhorn), the unglaciated region of Ohio, covering all or part of 33 counties, had 141 recorded families, 701 genera, and 2029 species. The total UpS sanctuary flora represents about 69% of the families, 34% of the genera, and 18% of the species of the region. In unglaciated Ohio, as in the UpS sanctuary, Asteraceae, Poaceae, Cyperaceae, Rosaceae, Fabaceae, and Lamiaceae were the most species-rich families, but the Cyperaceae and Fabaceae were more species-rich in the regional flora. In both floras, *Carex* was the most species-rich genus. However, the

genera *Crataegus*, *Viola*, and *Panicum* included many species regionally that were lacking at the UpS sanctuary.

Two local Ohio floras and one from southeastern Kentucky were used for smaller-scale comparisons: "The Ridges" in Athens County, Ohio (Kline 1994); Dysart Woods Laboratory in Belmont County, Ohio (Johnson 2001); and Lilley Cornett Woods in Letcher County, Kentucky (Sole et al. 1983). From each of these floras, only the forested areas were used for comparison. Therefore, if the flora contained species from old fields or other open areas, they were omitted. Similarly, the possible remnant prairie was omitted from the UpS sanctuary flora.

In comparison to similarly sized parcels, the forests of UpS were slightly more species-rich than "The Ridges" and Lilley Cornett Woods and most similar in family richness to "The Ridges" (Table 4). Dysart Woods Laboratory had fewer species and families but was also much smaller in size. The percentage of non-native plants at the UpS sanctuary, 8%, was comparatively low. All of the smaller-scale floras had a lower percentage of non-native species than the regional flora, presumably due to the fact that they did not include fields, roadsides, and other highly disturbed areas.

The rankings of families based on species richness were similar in all of these floras except that Lilley Cornett Woods had more Ericaceae than the Ohio floras, mostly due to the presence of several *Rhododendron* species that are not found in southeastern Ohio.

Possible remnant prairie. The presence of remnant prairies within the deciduous forests of Ohio is limited, and most are located in the central and western parts of the state (Transeau 1935). This does not mean that prairie habitat cannot be found in southeastern Ohio. Wistendahl (1975) described a remnant prairie, Buffalo Beats, in the northern part of Athens County based on the presence of several prairie species that are otherwise uncommon in the county.

When comparing the species of the possible remnant prairie to those found by Wistendahl (1975), there was only one species in common, *Amphicarpaea bracteata*. This species was common in most sanctuary habitats, so presence in this part of the sanctuary was not indicative of an unusual plant community. Furthermore, the UpS "prairie" did not have any of the typical, dominant grass species of mesic prairie habitats, such as *Andropogon gerardii*, *Sorghastrum nutans*, and *Panicum virgatum* (Weaver and Fitzpatrick 1934). Only a few species found in the possible prairie remnant (*Asclepias tuberosa*, *A. hirtella*, *Panicum lanuginosum*, *Pycnanthemum tenuifolium*, and *Rosa carolina*) were noted by Gleason

and Cronquist (1991) as being found in prairie habitats. Of these species, all but *A. hirtella* were also listed as occurring in habitats other than prairie.

Most of the species present in the possible prairie remnant in 2000–2001 were more characteristic of a disturbed area than prairie habitat. The percent of non-native species (15%) was almost twice as high as in the forested portions (8%). *Elaeagnus umbellata*, which was the dominant shrub, is an invasive species that was commonly planted on strip-mine spoils for erosion control and wildlife habitat (ODNAP 2000). Although the hilltop where the possible prairie remnant is located was not itself mined, much of the surrounding area was. If this part of the sanctuary ever supported prairie species they have now been eliminated. The current vegetation does not provide convincing evidence that it was once a prairie.

State-listed species. Both of the state-listed "potentially threatened" species were rare in the sanctuary. Only one population of *Corallorhiza wisteriana* was located, with approximately 40 individuals. This population was found on a high-elevation ridgetop, away from forest paths and regular human disturbance. The stand of *Juglans cinerea*, located on the forest edge, consisted of only a few individuals. The main threat to this species is from a canker fungus (Schneider 1993).

The UpS sanctuary network is unique in its focus on protecting habitat for native medicinal plants. At the sanctuary in Meigs County, Ohio, researchers study the population ecology and sustainability of the medicinal plant species. Educational workshops at this UpS sanctuary allow researchers and conservationists to share their work. This study has provided the first formal survey of the forests of the sanctuary. Based on comparisons of this flora with the regional flora and with other local floras of similar-sized areas, the flora of the sanctuary is typical of the region. The vegetation of the possible prairie remnant is more indicative of a disturbed area than a native prairie. The results of this study can be used as baseline data for future research at the sanctuary.

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APPENDIX

SPECIES DOCUMENTED AT THE UNITED PLANT SAVERS' SANCTUARY, MEIGS COUNTY, OHIO

The list is arranged alphabetically within divisions. Taxonomy and nomenclature follow Cooperrider et al. (2001) unless indicated with a dagger (†). Species preceded by an asterisk (*) are not native to southeastern Ohio (Cooperrider et al. 2001). Species preceded by a double asterisk (**) are native to southeastern Ohio, but the populations at the United Plant Savers' sanctuary are introduced. Species preceded by a PT are listed as potentially threatened within the state of Ohio (ODNAP 2002). The habitat of a species is indicated as follows: ridge top (R), slope (S), stream terrace (T), solely forest edge (E), solely on paths in the forest (Path), and possible remnant prairie (P). Collection numbers are those of the first author. Voucher specimens are deposited at the Bartley Herbarium at Ohio University (BHO).

LYCOPODIOPHYTA

LYCOPODIACEAE. *Diphasiastrum digitatum* (Dill. *ex* A. Braun) Holub – Infrequent; T, S, R; *142*.

POLYPODIOPHYTA

ADIANTACEAE. *Adiantum pedatum* L. – Infrequent; T; *479*.

ASPLENIACEAE. *Asplenium platyneuron* (L.) Britton, Sterns & Poggenb. Occasional; T, S, R, P; *108*. *Asplenium rhizophyllum* L. – Rare; T; *162*.

DENNSTAEDTIACEAE. *Dennstaedtia punctilobula* (Michx.) T. Moore – Rare; S; *645*.

DRYOPTERIDACEAE. *Athyrium filix-femina* (L.) Roth *ex* Mert. Rare; S; *701*. *Cystopteris protrusa* (Weath.) Blasdell – Rare; S; *650*. *Deparia acrostichoides* (Sw.) M. Kato – Occasional; T; *248*. *Diplazium pycnocarpon* (Spreng.) M. Broun – Rare;

T; *273. Dryopteris carthusiana* (Vill.) H. P. Fuchs – Frequent; T, S, R; *51. Dryopteris goldiana* (Hook. *ex* Goldie) A. Gray – Infrequent; T, S; *250. Dryopteris intermedia* (Muhl. *ex* Willd.) A. Gray – Infrequent; S; *259. Dryopteris marginalis* (L.) A. Gray – Rare; T; *394. Onoclea sensibilis* L. – Occasional; T, S; *580. Polystichum acrostichoides* (Michx.) Schott – Frequent; T, S, R, P; *52.*

OPHIOGLOSSACEAE. *Botrychium dissectum* Spreng. – Infrequent; S; *700. Botrychium virginianum* (L.) Sw. – Occasional; T, S; *575.*

POLYPODIACEAE. *Polypodium virginianum* L. – Infrequent; T; *237.*

THELYPTERIDACEAE. *Phegopteris hexagonoptera* (Michx.) Fée – Occasional; T, S; *413. Thelypteris noveboracensis* (L.) Nieuwl. – Occasional; T, S; *396.*

PINOPHYTA

CUPRESSACEAE. *Juniperus virginiana* L. – Infrequent; R, P; *328.*

PINACEAE. *Pinus virginiana* Mill. – Infrequent; R, P; *362.*

MAGNOLIOPHYTA

ACANTHACEAE. *Ruellia strepens* L. – Rare; S; *638.*

ACERACEAE. *Acer rubrum* L. – Frequent; T, S, R; *19. Acer saccharum* Marshall – Abundant; T, S, R; *11.*

ANACARDIACEAE. *Rhus copallina* L. – Rare; P; *332. Rhus glabra* L. – Infrequent; E; *292. Rhus typhina* L. – Infrequent; E; *671. Toxicodendron radicans* (L.) Kuntze – Occasional; T, S, R, P; no voucher.

ANNONACEAE. *Asimina triloba* (L.) Dunal – Frequent; T, S, R; *23.*

APIACEAE. *Cryptotaenia canadensis* (L.) DC. – Occasional; T, S; *87. *Daucus carota* L. – Infrequent; P; *656. Erigenia bulbosa* (Michx.) Nutt. – Occasional; T; *501. Osmorhiza claytonii* (Michx.) C. B. Clarke – Occasional; T, S; *244. Osmorhiza longistylis* (Torr.) DC. – Occasional; T, S; *583. Sanicula canadensis* L. – Frequent; T, S, R; *245. Sanicula gregaria* E. P. Bicknell – Occasional; T, S; *46. Sanicula trifoliata* E. P. Bicknell – Occasional; T, S; *266.*

APOCYNACEAE. *Apocynum cannabinum* L. – Rare; P; *134.*

ARACEAE. *Arisaema dracontium* (L.) Schott – Rare; T; no voucher. *Arisaema triphyllum* (L.) Schott – Occasional; T, S; *561.*

ARALIACEAE. *Aralia racemosa* L. – Rare; S; *390. Panax quinquefolius* L. – Occasional; T, S; *706.*

ARISTOLOCHIACEAE. *Aristolochia serpentaria* L. – Infrequent; S; no voucher. *Asarum canadense* L. – Frequent; T, S; *537*.

ASCLEPIADACEAE. *Asclepias hirtella* (Pennell) Woodson – Rare; R, P; *255*. *Asclepias quadrifolia* Jacq. – Rare; S; *599*. *Asclepias tuberosa* L. – Rare; P; *635*.

ASTERACEAE. *Achillea millefolium* L. – Rare; P; *130*. *Ambrosia artemisiifolia* L. – Infrequent; S, R, P; *462*. *Antennaria plantaginifolia* (L.) Richardson – Infrequent; S, R; *546*. *Aster cordifolius* L. – Occasional; S; *451*. *Aster divaricatus* L. – Occasional; T, S; *347*. *Aster lanceolatus* Willd. – Infrequent; S; *448*. *Aster lateriflorus* (L.) Britton – Infrequent; S; *421*. *Aster pilosus* Willd. – Rare; P; *713*. *Aster prenanthoides* Muhl. *ex* Willd. – Occasional; S; *426*. *Aster shortii* Lindl. – Occasional; S; *440*. *Bidens frondosa* L. – Occasional; T, S; *449*. **Chrysanthemum leucanthemum* L. – Occasional; R, P; *126*. **Cichorium intybus* L. – Rare; E; *699*. *Cirsium discolor* (Muhl. *ex* Willd.) Spreng. – Rare; E; *366*. *Elephantopus carolinianus* Raeusch. – Infrequent; S, P; *365*. *Erigeron annuus* (L.) Pers. – Rare; S, P; *205*. *Erigeron philadelphicus* L. – Infrequent; S; *27*. *Erigeron strigosus* Muhl. *ex* Willd. – Infrequent; P; *206*. *Eupatorium coelestinum* L. – Infrequent; S; *404*. *Eupatorium fistulosum* Barratt – Infrequent; E; *690*. *Eupatorium purpureum* L. – Infrequent; E; *692*. *†Eupatorium rugosum* Houtt. – Frequent; T, S, R, P; *220*. *Euthamia graminifolia* (L.) Nutt. – Rare; R; *693*. *Helianthus divaricatus* L. – Infrequent; S; *240*. **Hieracium caespitosum* Dumort. – Rare; P; *612*. *Hieracium scabrum* Michx. – Infrequent; E; *687*. *Hieracium venosum* L. – Infrequent; R; *38*. *Rudbeckia hirta* L. – Rare; E; *683*. *Senecio aureus* L. – Infrequent; E; *31*. *Solidago caesia* L. – Occasional; T, S; *436*. *Solidago flexicaulis* L. – Occasional; T; *453*. *Solidago juncea* Aiton – Occasional; R, P; *207*. *Solidago nemoralis* Aiton – Occasional; S, P; *360*. *Solidago ulmifolia* Muhl. *ex* Willd. – Occasional; S; *341*. **Taraxacum officinale* Weber *ex* F. H. Wigg. – Rare; S; *551*. *Verbesina alternifolia* (L.) Britton *ex* Kearney – Infrequent; S; *313* . *Vernonia gigantea* (Walter) Trel. *ex* Branner & Coville – Infrequent; E; *406*.

BALSAMINACEAE. *Impatiens capensis* Meerb. – Frequent; T, S, R; *160*. *Impatiens pallida* Nutt. – Occasional; T, S; *156*.

BERBERIDACEAE. **Berberis thunbergii* DC. – Infrequent; S; *544*. *Caulophyllum thalictroides* (L.) Michx. – Frequent; T, S; *516*. *Jeffersonia diphylla* (L.) Pers. – Occasional; T, S; *80*. *Podophyllum peltatum* L. – Frequent; T, S, R, P; *572*.

BETULACEAE. *Carpinus caroliniana* Walter – Occasional; T, S, R; *276*. *Ostrya virginiana* (Mill.) K. Koch – Frequent; T, S, R; *309*.

BIGNONIACEAE. *Campsis radicans* (L.) Seem. *ex* Bureau – Rare; E; *672*.

BORAGINACEAE. *Cynoglossum virginianum* L. – Occasional; S, R; *576*. *Hackelia virginiana* (L.) I. M. Johnst. – Infrequent; T; *213*. *Myosotis macrosperma* Engelm. – Infrequent; T, S, R; *568*.

BRASSICACEAE. **Barbarea vulgaris* R. Br. – Infrequent; E; *18*. *Cardamine concatenata* (Michx.) Sw. – Frequent; T, S, R; *506*. *Cardamine douglassii* Britton – Occasional; T, S; *500*. **Cardamine hirsuta* L. – Infrequent; T, S; *4*. *Cardamine*

pensylvanica Muhl. *ex* Willd. – Rare; T; *579*. **Lepidium campestre* (L.) R. Br. – Rare; P; *132*.

CAESALPINIACEAE. *Cercis canadensis* L. – Infrequent; T, S, R, P; *17*. *Gleditsia triacanthos* L. – Infrequent; S; *684*.

CAMPANULACEAE. *Campanula americana* L. – Infrequent; T, S; *193*. *Lobelia inflata* L. – Occasional; T, S, R, P; *224*. *Lobelia siphilitica* L. – Rare; Path; *422*.

CAPRIFOLIACEAE. **Lonicera japonica* Thunb. – Infrequent; S, R, P; *53*. *Sambucus canadensis* L. – Infrequent; E; *54*. *Triosteum angustifolium* L. – Occasional; T, S; *275*. *Viburnum acerifolium* L. – Occasional; T, S, R; *41*. *Viburnum prunifolium* L. – Occasional; S; *446*.

CARYOPHYLLACEAE. **Dianthus armeria* L. – Infrequent; S, R, P; *136*. *Paronychia canadensis* (L.) Alph. Wood – Occasional; S; *191*. *Silene virginica* L. – Infrequent; S, R; *25*. **Stellaria media* (L.) Vill. – Infrequent; S, R; *5*.

CELASTRACEAE. *Celastrus scandens* L. – Rare; S; *428*.

CLUSIACEAE. *Hypericum drummondii* (Grev. & Hook.) Torr. & A. Gray – Rare; R; *694*. *Hypericum mutilum* L. – Infrequent; Path; *308*. **Hypericum perforatum* L. – Infrequent; P; *644*. *Hypericum prolificum* L. – Rare; P; *214*. *Hypericum punctatum* Lam. – Occasional; S, R, P; *209*.

COMMELINACEAE. **Commelina communis* L. – Rare; S; *288*. *Tradescantia virginiana* L. – Infrequent; R; *40*.

CONVOLVULACEAE. *Calystegia spithamaea* (L.) Pursh – Rare; P; *615*. *Ipomoea pandurata* (L.) G. Mey. – Infrequent; S, P; *222*.

CORNACEAE. *Cornus alternifolia* L. f. – Rare; T; *704*. *Cornus florida* L. – Infrequent; T, S, R; *7*. *Nyssa sylvatica* Marshall – Infrequent; T, S; *655*.

CRASSULACEAE. *Sedum ternatum* Michx. – Occasional; T, S; *21*.

CYPERACEAE. *Carex albicans* Willd. *ex* Spreng. – Rare; T, S; *513*. *Carex albursina* E. Sheld. – Occasional; T, S, R; *563*. *Carex blanda* Dewey – Occasional; S; *16*. *Carex careyana* Torr. *ex* Dewey – Occasional; T, S; *532*. *Carex cephalophora* Muhl. *ex* Willd. – Occasional; P; *122*. *Carex frankii* Kunth – Rare; T, S; *152*. *Carex hirsutella* Mack. – Occasional; R, P; *48*. *Carex jamesii* Schwein. – Infrequent; S; *83*. *Carex laxiflora* Lam. – Infrequent; T, S; *540*. *Carex pensylvanica* Lam. – Occasional; R; *36*. *Carex rosea* Schkuhr *ex* Willd. – Occasional; T, R, S; *592*. *Carex sparganioides* Muhl. *ex* Willd. – Rare; S; *616*. *Carex vulpinoidea* Michx. – Infrequent; S; *146*. *Carex woodii* Dewey – Infrequent; R; *565*. *Scirpus cyperinus* (L.) Kunth – Infrequent; S; *233*. *Scirpus polyphyllus* Vahl – Rare; S; *144*.

DIOSCOREACEAE. *Dioscorea villosa* L. – Occasional; S; *678*.

EBENACEAE. *Diospyros virginiana* L. – Rare; P; *474*.

ELAEAGNACEAE. **Elaeagnus umbellata* Thunb. – Occasional; S, R, P; *32*.

ERICACEAE. *Oxydendrum arboreum* (L.) DC. – Occasional; S, R; *336*. *Vaccinium pallidum* Aiton Rare; R; *34*. *Vaccinium stamineum* L. – Occasional; R; *37*.

EUPHORBIACEAE. *Acalypha virginica* L. – Infrequent; S, R; *264*.

FABACEAE. *Amphicarpaea bracteata* (L.) Fernald – Occasional; T, S, R, P; *703*. *Desmodium ciliare* (Muhl. *ex* Willd.) DC. – Rare; P; *358*. *Desmodium nudiflorum* (L.) DC. – Occasional; T, S, R, P; *230*. *Desmodium paniculatum* (L.) DC. Occasional; T, S, R; *298*. *Desmodium pauciflorum* (Nutt.) DC. – Rare; T, S; *247*. *Desmodium rotundifolium* DC. Rare; R; *326*. *Desmodium viridiflorum* (L.) DC. Infrequent; S; *282*. *Desmodium* sp. Infrequent; T; *399*. *Lespedeza hirta* (L.) Hornem. – Rare; S; *343*. *Lespedeza intermedia* (S. Watson) Britton – Rare; P; *356*. **Melilotus officinalis* (L.) Pall. – Rare; E; *624*. *Robinia pseudoacacia* L. – Occasional; S; *588*. **Trifolium campestre* Schreb. – Infrequent; P; *138*. **Trifolium repens* L. – Infrequent; E; *657*. *Vicia caroliniana* Walter – Rare; R; *555*.

FAGACEAE. **Castanea mollissima* Blume – Rare; E; *629* [Planted; Paul Strauss, UpS, pers. comm.]. *Fagus grandifolia* Ehrh. – Frequent; T, S, R; *386*. *Quercus alba* L. – Abundant; T, S, R, P; *470*. *Quercus prinus* L. – Frequent; T, S, R; *384*. *Quercus rubra* L. – Abundant; T, S, R, P; *189*. *Quercus velutina* Lam. – Abundant; T, S, R, P; *290*.

FUMARIACEAE. *Corydalis flavula* (Raf.) DC. – Rare; S; *526*. *Dicentra canadensis* (Goldie) Walp. – Rare; S; *535*. *Dicentra cucullaria* (L.) Bernh. – Occasional; T, S; *517*.

GENTIANACEAE. *Obolaria virginica* L. – Rare; R; *570*. *Sabatia angularis* (L.) Pursh – Rare; P; *696*.

GERANIACEAE. **Geranium columbinum* L. – Rare; E; *223*. *Geranium maculatum* L. – Occasional; T, S, R; *19*.

HIPPOCASTANACEAE. *Aesculus flava* Aiton – Frequent; T, S; *411*.

HYDRANGEACEAE. *Hydrangea arborescens* L. – Occasional; T; *150*.

HYDROPHYLLACEAE. *Hydrophyllum macrophyllum* Nutt. Occasional; T, S; *58*. *Hydrophyllum virginianum* L. Occasional; S; *91*.

IRIDACEAE. *Sisyrinchium angustifolium* Mill. – Infrequent; T, S; *195*.

JUGLANDACEAE. *Carya cordiformis* (Wangenh.) K. Koch – Frequent; T, S, R; *441*. *Carya glabra* (Mill.) Sweet Occasional; S, R; *466*. *Carya ovata* (Mill.) K. Koch – Abundant; T, S, R, P; *430*. *Carya tomentosa* (Poir.) Nutt. – Rare; P; *478*. PT *Juglans cinerea* L. – Rare; S; *658*. *Juglans nigra* L. – Occasional; S; *679*.

JUNCACEAE. *Juncus effusus* L. – Infrequent; P; *128. Juncus tenuis* Willd. Infrequent; S, R; *106. Luzula echinata* (Small) F. J. Herm. – Occasional; T, S; *512.*

LAMIACEAE. *Agastache nepetoides* (L.) Kuntze – Rare; Path; *311. Blephilia hirsuta* (Pursh) Benth. – Rare; T; *271. Clinopodium vulgare* L. – Rare; P; *698. Collinsonia canadensis* L. – Infrequent; T, S; *415. Cunila origanoides* (L.) Britton – Frequent; S, R; *321. *Glechoma hederacea* L. – Infrequent; Path; *610. Hedeoma pulegioides* (L.) Pers. – Infrequent; S; *306. *Lamium purpureum* L. – Infrequent; S; *8. Lycopus virginicus* L. – Infrequent; S; *427. Monarda fistulosa* L. – Rare; E; *659. Prunella vulgaris* L. – Occasional; S, P; *201. Pycnanthemum tenuifolium* Schrad. – Rare; P; *199. Salvia lyrata* L. – Rare; S; *605. Scutellaria lateriflora* L. – Rare; E; *400. Scutellaria nervosa* Pursh – Infrequent; T; *604. Scutellaria ovata* Hill – Rare; S; *702. Scutellaria serrata* Andrews – Occasional; T, S; *600. Teucrium canadense* L. – Rare; Path; *653.*

LAURACEAE. *Lindera benzoin* (L.) Blume – Abundant; T, S, R, P; *509. Sassafras albidum* (Nutt.) Nees – Frequent; T, S, R, P; *472.*

LILIACEAE. *Allium tricoccum* Aiton – Occasional; T, S; *226. *Allium vineale* L. – Infrequent; T; *56. **Chamaelirium luteum* (L.) A. Gray – Rare; S; no voucher. *Erythronium albidum* Nutt. – Rare; S; *510. Erythronium americanum* Ker Gawl. – Occasional; T, S; *519. Polygonatum biflorum* (Walter) Elliott – Occasional; T, S, R; *601. Smilacina racemosa* (L.) Desf. – Frequent; T, S, R, P; *560. Trillium grandiflorum* (Michx.) Salisb. – Occasional; T, S; *14. Trillium sessile* L. – Rare; T; *30. Uvularia grandiflora* Sm. – Occasional; T, S; *552.*

LIMNANTHACEAE. *Floerkea proserpinacoides* Willd. – Infrequent; T; *543.*

MAGNOLIACEAE. *Liriodendron tulipifera* L. – Abundant; T, S, R, P; *42 Magnolia acuminata* (L.) L. – Rare; T; *654.*

MENISPERMACEAE. *Menispermum canadense* L. – Occasional; T, S; *640.*

MONOTROPACEAE. *Monotropa uniflora* L. – Infrequent; T, S, R; *180.*

MORACEAE. *Maclura pomifera* (Raf.) C. K. Schneid. – Rare; P; *256. Morus rubra* L. – Rare; S; *617.*

OLEACEAE. *Fraxinus americana* L. – Occasional; T, S; *460. Fraxinus pennsylvanica* Marshall – Occasional; T, S, R, P; *392. Fraxinus quadrangulata* Michx. – Occasional; T, S, R; *239.*

ONAGRACEAE. *Circaea lutetiana* L. – Occasional; T, S, R, P; *158. Epilobium coloratum* Biehler – Rare; E; *424. Ludwigia alternifolia* L. – Rare; E; *688.*

ORCHIDACEAE. *Aplectrum hyemale* (Muhl. *ex* Willd.) Torr. – Infrequent; T, S; *609. Corallorhiza odontorhiza* (Willd.) Poir. – Infrequent; T, S; *349.* PT *Corallorhiza wisteriana* Conrad – Rare; R; *571. **Cypripedium parviflorum* Salisb. – Rare; T; no

voucher. *Goodyera pubescens* (Willd.) R. Br. *ex* W. T. Aiton – Infrequent; T, S; *408*. *Spiranthes vernalis* Engelm. & A. Gray – Rare; S; *465*.

OROBANCHACEAE. *Conopholis americana* (L.) Wallr. Occasional; T, S, R; *597*. *Epifagus virginiana* (L.) Barton – Frequent; T, S; *346*.

OXALIDACEAE. *Oxalis dillenii* Jacq. – Occasional; T, S, R; *35*. *Oxalis violacea* L. – Infrequent; S, R; *39*.

PAPAVERACEAE. *Sanguinaria canadensis* L. – Occasional; T, S; *504*.

PASSIFLORACEAE. *Passiflora lutea* L. – Rare; S; *674*.

†**PHRYMACEAE.** *Phryma leptostachya* L. – Occasional; T, S; *186*.

PHYTOLACCACEAE. *Phytolacca americana* L. – Occasional; S; *285*.

PLANTAGINACEAE. **Plantago lanceolata* L. – Infrequent; Path; *681*. *Plantago rugelii* Decne. – Infrequent; Path; *301*.

PLATANACEAE. *Platanus occidentalis* L. – Infrequent; T, S, R; *626*.

POACEAE. *Agrostis perennans* (Walter) Tuck. Occasional; S, R, P; *330*. *Andropogon virginicus* L. Infrequent; P; *476*. *Brachyelytrum erectum* (Schreb. *ex* Spreng.) P. Beauv. Occasional; T, S, R; *176*. *Bromus pubescens* Muhl. *ex* Willd. Occasional; S, R; *47*. *Cinna arundinacea* L. Infrequent; Path; *303*. **Dactylis glomerata* L. Infrequent; P; *140*. *Danthonia spicata* (L.) P. Beauv. *ex* Roem. & Schult. – Occasional; S, R, P; *49*. *Diarrhena americana* P. Beauv. – Occasional; S, R, P; *112*. *Echinochloa muricata* (P. Beauv.) Fernald – Rare; S; *388*. *Elymus hystrix* L. – Occasional; T, S, R, P; *114*. *Elymus villosus* Muhl. *ex* Willd. – Occasional; T, S, R; *182*. *Festuca subverticillata* (Pers.) E. B. Alexeev – Infrequent; T; *94*. *Glyceria striata* (Lam.) Hitchc. – Infrequent; T, R; *148*. **Holcus lanatus* L. – Rare; E; *685*. *Leersia virginica* Willd. – Infrequent; T; *278*. *Panicum acuminatum* Sw. – Infrequent; S, R, P; *124*. *Panicum boscii* Poir. – Occasional; S, R, P; *324*. *Panicum clandestinum* L. Infrequent; S, R; *630*. *Panicum dichotomum* L. Infrequent; R; *372*. **Phleum pratense* L. – Infrequent; E; *216*. **Poa compressa* L. – Occasional; S, R; *50*. *Poa cuspidata* Nutt. – Occasional; T, S, R; *511*. *Poa sylvestris* A. Gray – Occasional; T; *606*. *Tridens flavus* (L.) Hitchc. Rare; P; *253*.

POLEMONIACEAE. *Phlox divaricata* L. – Occasional; T, S, R; *1*. *Polemonium reptans* L. – Occasional; T, S, R; *15*.

POLYGALACEAE. *Polygala sanguinea* L. – Rare; P; *218*. *Polygala verticillata* L. – Rare; Path; *307*.

POLYGONACEAE. **Polygonum caespitosum* Blume – Occasional; T, S, R, P; *168*. *Polygonum punctatum* Elliott – Occasional; T, S; *228*. *Polygonum sagittatum* L. – Rare; T, S; *338*. *Polygonum scandens* L. – Rare; E; *378*. *Polygonum virginianum* L. – Occasional; T, S, R, P; *260*. **Rumex* sp. – Rare; S; *647*.

PORTULACACEAE. *Claytonia virginica* L. – Frequent; T, S, R; *6*.

PRIMULACEAE. *Lysimachia ciliata* L. – Rare; T; *270*.

PYROLACEAE. *Chimaphila maculata* (L.) Pursh – Occasional; R; *166*.

RANUNCULACEAE. *Actaea pachypoda* Elliott – Occasional; T, S; *258*. *Anemone virginiana* L. – Occasional; S; *296*. *Cimicifuga racemosa* (L.) Nutt. – Frequent; T, S, R; *178*. *Delphinium tricorne* Michx. – Occasional; T, S, R; *20*. *Hepatica acutiloba* DC. – Frequent; T, S; *503*. *Hydrastis canadensis* L. – Occasional; T, S, R; *541*. *Ranunculus abortivus* L. – Occasional; S; *3*. *Ranunculus micranthus* Nutt. – Occasional; S; *558*. *Thalictrum dioicum* L. – Infrequent; T, S; *554*. *Thalictrum thalictroides* (L.) A. J. Eames & B. Boivin – Occasional; T, S, R; *22*.

ROSACEAE. *Agrimonia parviflora* Aiton – Infrequent; R, P; *402*. *Agrimonia pubescens* Wallr. – Occasional; T, S, R; *197*. *Amelanchier arborea* (F. Michx.) Fernald – Occasional; S, R; *242*. *Crataegus pruinosa* (H. L. Wendl.) K. Koch – Infrequent; R; *370*. *Crataegus* sp. – Infrequent; S; *424*. *Geum canadense* Jacq. – Frequent; T, S, R; *164*. *Geum vernum* (Raf.) Torr. & A. Gray – Occasional; T, S, R; *12*. *Malus coronaria* (L.) Mill. – Rare; E; *33*. *Porteranthus stipulatus* (Muhl. *ex* Willd.) Britton – Occasional; S, R; *188*. *Potentilla simplex* Michx. – Occasional; T, S, R; *44*. *Prunus serotina* Ehrh. – Occasional; T, S; *686*. *Rosa carolina* L. – Infrequent; R, P; *105*. **Rosa multiflora* Thunb. *ex* Murray – Frequent; T, S, R, P; *593*. *Rosa setigera* Michx. – Rare; E; *627*. *Rubus allegheniensis* Porter – Frequent; T, S, R, P; *591*. *Rubus flagellaris* Willd. – Occasional; S, R; *43*. *Rubus occidentalis* L. – Occasional; T, S, R, P; *608*. *Spiraea tomentosa* L. – Infrequent; S, R; *231*.

RUBIACEAE. *Galium aparine* L. – Occasional; T, S, R; *9*. *Galium circaezans* Michx. – Occasional; T, S, R; *45*. *Galium concinnum* Torr. & A. Gray – Frequent; T, S, R; *154*. *Galium pilosum* Aiton – Infrequent; S, P; *203*. *Galium triflorum* Michx. – Frequent; T, S, R; *174*. *Houstonia caerulea* L. – Infrequent; S; *24*. *Houstonia longifolia* Gaertn. – Occasional; S, R, P; *116*. *Mitchella repens* L. – Rare; T; *652*.

SALICACEAE. *Populus grandidentata* Michx. – Occasional; T, S, R; *334*. *Salix nigra* Marshall – Infrequent; E; *26*.

SAXIFRAGACEAE. *Heuchera americana* L. – Infrequent; T, S; *594*. *Saxifraga virginiensis* Michx. – Occasional; T, S, R; *28*.

SCROPHULARIACEAE. *Mimulus alatus* Aiton – Rare; S; *695*. *Penstemon digitalis* Nutt. *ex* Sims – Infrequent; S, R; *57*.

SIMAROUBACEAE. **Ailanthus altissima* (Mill.) Swingle – Rare; E; *675*.

SMILACACEAE. *Smilax glauca* Walter – Rare; S, R, P; *613*. *Smilax hispida* Muhl. *ex* Torr. – Infrequent; T, S; *611*. *Smilax rotundifolia* L. – Frequent; T, S, R, P; *318*.

SOLANACEAE. *Solanum carolinense* L. – Infrequent; S, P; *211*. *Solanum nigrum* L. – Rare; S; *419*.

STAPHYLEACEAE. *Staphylea trifolia* L. – Occasional; T; *417*.

TILIACEAE. *Tilia americana* L. – Occasional; T, S, R; *639*.

ULMACEAE. *Celtis occidentalis* L. – Occasional; T, S, R; *422*. *Ulmus americana* L. – Occasional; T, S, R, P; *445*. *Ulmus rubra* Muhl. – Occasional; T, S; *444*.

URTICACEAE. *Boehmeria cylindrica* (L.) Sw. – Occasional; T; *261*. *Laportea canadensis* (L.) Wedd. – Frequent; T; *257*. *Pilea pumila* (L.) A. Gray – Frequent; T, S; *352*.

VALERIANACEAE. *Valerianella chenopodiifolia* (Pursh) DC. – Rare; S; *559*.

VERBENACEAE. *Verbena urticifolia* L. – Infrequent; S, P; *287*.

VIOLACEAE. *Viola canadensis* L. – Frequent; T, S; *10*. *Viola pubescens* Aiton – Occasional; T, S; *2*. *Viola sororia* Willd. – Occasional; T, S, R; *13*. *Viola striata* Aiton – Frequent; T, S; *29*.

VITACEAE. *Parthenocissus quinquefolia* (L.) Planch. – Frequent; T, S, R, P; *643*. *Vitis aestivalis* Michx. – Infrequent; T, R, P; *97*. *Vitis vulpina* L. – Occasional; S, R; *55*.

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NOTE

VASCULAR PLANTS OF THE ISLAND OF NEWFOUNDLAND, CANADA: RECENT ADDITIONS AND REDISCOVERIES

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The Newfoundland Rare Plant Project (NFRPP) was initiated in 1999 as a multi-partnered effort led by the Newfoundland and Labrador Department of Tourism, Culture and Recreation, the Atlantic Canada Conservation Data Centre, and the Institut de recherche en biologie végétale of the Université de Montréal. The main goals of the project have been to update the previous list of rare vascular plants of the Island (Bouchard et al. 1991) and to obtain data to support management efforts towards the conservation of rare plants.

During its initial three years (1999 to 2001), the NFRPP conducted a major new inventory of the vascular plants of the Island of

Newfoundland. This was done primarily through intensive, targeted field surveys in the western, central, and northeastern regions of the Island. Work also involved reevaluation of the relevant literature and verification of some critical herbarium specimens at the Provincial Museum of Newfoundland and Labrador (NFM) and the Herbier Marie Victorin of the Université de Montréal (MT). Since 2001, individuals and institutions involved in the NFRPP have continued to collect and compile information on vascular plants throughout the province of Newfoundland and Labrador.

The list provided here adds to the *Annotated Checklist of the Vascular Plants of Newfoundland and Labrador* (Meades et al. 2000), which already incorporates some of the early findings of the NFRPP. So far, the NFRPP has recorded twelve vascular plant taxa new to the Island of Newfoundland. Eleven of these are considered native: *Symphyotrichum boreale*, *S. tradescantii*, *Lechea intermedia*, *Bartonia virginica*, *Proserpinaca pectinata*, *Carex radiata*, *C. retrorsa*, *Eleocharis erythropoda*, *Scirpus pedicellatus*, *Potamogeton richardsonii*, and *P. robbinsii*. One more, *Hypericum pulchrum*, is considered introduced. The NFRPP has also rediscovered six rare vascular plant taxa previously known for the Island only from historical records: *Equisetum hyemale* subsp. *affine*, *Oclemena acuminata*, *Symphyotrichum ciliolatum*, *Ranunculus recurvatus* var. *recurvatus*, *Carex petricosa* var. *misandroides*, and *Juncus subcaudatus*.

A more detailed account for each of the taxa listed above is provided in the following "Species Accounts" section. Families are presented in the same order as in Meades et al. (2000). Nomenclature follows Meades et al. (2000) for taxa included therein, the *Flora of North America* for species of Potamogetonaceae and Cyperaceae new to Newfoundland, and Kartesz (1999) for additional species new to Newfoundland. Voucher specimens are variously deposited in NFM, MT, and the herbarium of Sir Wilfred Grenfell College, Corner Brook, Newfoundland.

SPECIES ACCOUNTS

Species new to the Island of Newfoundland are marked with an asterisk. To protect sensitive location data, the wording of some location descriptions has been shortened, and some latitude and longitude coordinates have been rounded to the nearest minute. Square brackets have been used where the numerical precision of specimen citation data has been reduced.

EQUISETACEAE

Equisetum hyemale L. subsp. *affine* (Engelm.) Calder & Roy L. Taylor

SPECIMEN CITATION: CANADA. Newfoundland: St. George's Bay, Fishells Brook, near mouth [48°19′N, 58°42′W], 9 Sep 2000, *N. Djan-Chékar & C. Hanel NDC 00-1581* (NFM, MT).

The only previous Newfoundland collection of this taxon was made in central Newfoundland in 1910 [Middle Birchy Pond, 11 Jul 1910, *M. L. Fernald & K. M. Wiegand 2364* (GH)]. Unfortunately the identity of the specimen is questionable (Bouchard et al. 1991). Hauke (1963) referred it to *Equisetum* ×*trachyodon* A. Braun, a hybrid between *E. hyemale* and *E. variegatum* Schleich. Subsequently, Hauke (1993) included Newfoundland in the distribution of *E. hyemale* subsp. *affine* without any comment. The new population reported here was found on the sandy and gravelly bank of Fischells Brook on the west coast of the Island, almost 200 km from the original locality.

ASTERACEAE

Oclemena acuminata (Michx.) Greene (= *Aster acuminatus* Michx.)

SPECIMEN CITATIONS: CANADA. Newfoundland: Southwest coast, J. T. Cheeseman Provincial Park, [47°38′N, 59°15′W], 3 Aug 2000, *C. Hanel & S. Powell CH 000803-5* (NFM, MT); Southwest coast, Port aux Basques area, [approx. 2 km] N of the turnoff to J. T. Cheeseman Provincial Park, [47°38′N, 59°14′W], 23 Sep 2002, *C. Hanel CH 020923-3* (NFM).

Common in eastern North America, this species was previously known from only two localities in western Newfoundland, both historical [Lark Mountain, 4 Sep 1926, *M. L. Fernald, B. Long & J. M. Fogg 460* (GH); Port aux Basques (back of), 31 Aug 1924, *M. L. Fernald, B. Long & B. Dunbar 27139* (GH)]. The recent collections are both from the same general locality on the southwest coast of the Island, probably very close to the site of Fernald's Port aux Basques collection.

**Symphyotrichum boreale* (Torr. & A. Gray) Á. Löve & D. Löve (= *Aster borealis* Provanch.)

SPECIMEN CITATION: CANADA. Newfoundland: Bay of Islands, Humber Arm, Wild Cove Brook, [48°58′N, 57°52′W], 4 Sep 2000, *N. Djan-Chékar, C. Hanel & H. Mann NDC 00-1461* (NFM, MT, Sir Wilfred Grenfell College).

A somewhat calciphilic fen species found throughout boreal and montane North America. This first Newfoundland collection is from

a rich fen on the central west coast, near Corner Brook. The species was previously known to occur as far east as Cape Breton Island, Nova Scotia (Zinck 1998).

Symphyotrichum ciliolatum (Lindl. *ex* Hook.) Á. Löve & D. Löve (— *Aster ciliolatus* Lindl.)

SPECIMEN CITATION: CANADA. Newfoundland: Stephenville Area, Romaine's Brook, [48°33′N, 58°40′W], 14 Jul 1999, *C. Hanel CH 990714-1* (NFM).

Previous to the NFRPP, the probable existence of this species on the Island of Newfoundland had been documented only once through the type of *Aster subgeminatus* Fernald [Table Mountain, 16 Aug 1910, *M. L. Fernald, K. M. Wiegand & J. Kittredge 4126* (GH)], which now appears to be a hybrid between *Symphyotrichum ciliolatum* and *S. novi-belgii* (L.) G. L. Nesom var. *novi-belgii*. The collection reported here is a good representative of the species. It was found in the forested floodplain of Romaine's Brook, near Table Mountain, on the west coast of the Island. At Romaine's Brook, *S. ciliolatum* does seem to hybridize with *S. novi-belgii*, supporting the probable hybrid status of Fernald's specimen. The species is somewhat calciphilic, and the area where it was discovered in Newfoundland is underlain by limestone.

**Symphyotrichum tradescantii* (L.) G. L. Nesom (=*Aster tradescantii* L.)

SPECIMEN CITATIONS: CANADA. Newfoundland: Head of St. George's Bay, Bottom Brook, First Pond, 48°31′N, 58°16′W, 15 Jul 1999, *J. E. Maunder NFM 6721* (NFM); Bay St. George, Southwest Brook, [near] TCH bridge over brook, [48°30′N, 58°16′W], 30 Jul 2000, *C. Hanel & S. Powell CH 000730-36* (NFM); Southern Long Range Mountains, Bottom Brook, upstream from Third Pond, [48°32′N, 58°12′W], 13 Sep 2000, *N. Djan-Chékar & D. Brake NDC 00-1728* (NFM, MT).

This species was reported from southern Newfoundland by Fernald (1950). However, the report was rejected by Meades et al. (2000) owing to the absence of verified specimens. The specimens listed here were collected by the NFRPP on sandy riverbanks and lake shores near the head of St. George's Bay in western Newfoundland, finally confirming the presence of the species on the Island.

CISTACEAE

**Lechea intermedia* Legg. *ex* Britton

SPECIMEN CITATION: CANADA. Newfoundland: Exploits Valley, Grand Falls, W of community, Exploits River, [near] mouth of Thunder Brook, [48°56′N, 55°49′W], 30 Aug 2001, *C. Hanel & J. Hancock CH 010830-15* (NFM, MT).

This species is widely distributed in eastern parts of southern Canada and the northern United States (Scoggan 1978). The specimen from Grand Falls in central Newfoundland was collected in gravel and cobbles on a sloping riverbank. The next nearest records are from Cape Breton Island, Nova Scotia (Zinck 1998).

HYPERICACEAE

**Hypericum pulchrum* L.

SPECIMEN CITATION: CANADA. Newfoundland: Bay St. George, Black Duck, [shore of Harry's River], [48°34′N, 58°22′W], 21 Jul 2000, *C. Hanel & S. Powell CH 000727-17* (NFM, MT).

This species is native to Eurasia. The only previous report for North America is from Saint-Pierre et Miquelon (Meades et al. 2000). The Newfoundland specimen was found at Black Duck, on the west coast of the Island, in an old abandoned field.

GENTIANACEAE

**Bartonia virginica* (L.) Britton, Sterns & Poggenb.

SPECIMEN CITATIONS: CANADA. Newfoundland: Codroy Valley, N of Doyles along the TCH, [47°51′N, 59°9′W], 8 Sep 2000, *N. Djan-Chékar, C. Hanel & H. Mann NDC 00-1563* (NFM, MT); South Coast, Burgeo, ~5 km WNW of, [47°37′N, 57°41′W], 13 Aug 2000, *C. Hanel CH 000813-1* (NFM).

This species is an Atlantic coastal plain element of the eastern North American flora. As reported by Meades et al. (2000), it was first collected in Newfoundland, by the NFRPP, in 2000. Both collections were from open, acidic habitats (rocky heath and bog) in southern regions of the Island. The species was already known from nearby Saint-Pierre et Miquelon (Rouleau and Lamoureux 1992).

HALORAGACEAE

**Proserpinaca pectinata* Lam.

SPECIMEN CITATION: CANADA. Newfoundland: Southern Long Range Mountains, Bottom Brook, upstream from Third Pond, [48°32′N, 58°12′W], 13 Sep 2000, *N. Djan-Chékar & D. Brake NDC 00-1720* (NFM, MT).

This is a species of the Atlantic coastal plain of North America. It was unknown from Newfoundland until the NFRPP made this collection at Bottom Brook, near the head of St. George's Bay on the west coast of the Island. Plants were growing in mats of aquatic vegetation rooted in

soft sandy mud on a riverbank. The next nearest records are from Nova Scotia (Crow and Hellquist 2000).

RANUNCULACEAE

Ranunculus recurvatus Poir. *in* Lam. var. *recurvatus*

SPECIMEN CITATION: CANADA. Newfoundland: Serpentine Lake, Blue Hill Brook, [48°53′N, 58°19′W], 13 Aug 1999, *L. Brouillet, S. Hay & D. Ballam LB 99-224* (NFM).

This taxon had last been collected in Newfoundland in 1962 [Sheep Brook, 1962, *E. Rouleau 7633* (MT)]. As indicated by Meades et al. (2000), it was rediscovered by the NFRPP, in 1999, in an alder swamp at Serpentine Lake, a new locality for the taxon in western Newfoundland. The specimen documents the report by Meades et al. (2000).

CYPERACEAE

Carex petricosa Dewey var. *misandroides* (Fernald) B. Boivin

SPECIMEN CITATION: CANADA. Newfoundland: Bay of Islands, Goose Arm, William Wheeler Point, [49°10′N, 57°52′W], 21 Jul 2000, *N. Djan-Chékar, J. Maunder, L. Brouillet & C. Wentzell NDC 00-424B* (NFM, MT).

This sedge is rare in Canada. It is an eastern North American endemic known only from northern Québec, the Gaspé Peninsula, and western Newfoundland (Bouchard et al. 1991; Labrecque and Lavoie 2002). It had not been collected in Newfoundland since the late 1960s [Table Mountain (summit), Pine Tree, 19 Jul 1967, *E. Rouleau 10863* (MT)]. The population reported here was originally discovered by Ernest Rouleau in 1948 [Goose Arm, William Wheeler Point, Jul 1948, *E. Rouleau 184* (MT)].

**Carex radiata* (Wahlenb.) Small

SPECIMEN CITATION: CANADA. Newfoundland: Bay of Islands, Humber Arm, Wild Cove Brook, [48°58′N, 57°53′W], 19 Jul 2000, *N. Djan-Chékar, C. Hanel, L. Brouillet, J. Maunder, C. Wentzell & S. Powell NDC 00-375* (NFM, MT, Sir Wilfred Grenfell College).

This species is known from deciduous and mixed forests in eastern North America (Ball 2002). John Bell collected a Newfoundland specimen in 1867 [Great Codroy River, 10 Jul 1867, *J. Bell s.n.* (MT)]. Bell originally identified it as *Carex rosea* Schkuhr, a name that has been frequently misapplied to *C. radiata* (Ball 2002). Ernest Rouleau

later reexamined Bell's specimen and assigned it to *C. cephalantha* E. P. Bicknell. As a consequence, *C. radiata* has never been included in plant lists for Newfoundland and Labrador (Meades et al. 2000; Robertson 1984; Rouleau 1978; Rouleau and Lamoureux 1992). The collection by the NFRPP, in alluvial thickets at Wild Cove Brook, on the Island's west coast, led to the reidentification of Bell's 1867 specimen as *C. radiata*.

**Carex retrorsa* Schwein.

SPECIMEN CITATION: CANADA. Newfoundland: Long Range Mountains, Deer Lake, shore at mouth of Upper Humber River, [49°10′N, 57°28′W], 29 Aug 2000, *N. Djan-Chékar, C. Hanel, L. Lavers, H. Mann & C. Wentzell NDC 00-1300* (NFM).

This species occurs in wet habitats across North America (Reznicek and Ford 2002). It was reported for Newfoundland by Scoggan (1978), but Meades et al. (2000) rejected the report because no voucher could be found in herbaria. Reznicek and Ford (2002) also omitted the Newfoundland report. The collection made by the NFRPP on the shores of Deer Lake confirms the occurrence of the species on the Island.

**Eleocharis erythropoda* Steud.

SPECIMEN CITATION: CANADA. Newfoundland: Northeast coast, New World Island, Summerford, SE of, [49°29′N, 54°46′W], 22 Jul 2001, *C. Hanel & S. Pardy CH 010722-11* (NFM, MT).

Two *Eleocharis* collections from western Newfoundland [Serpentine Lake (western end of), 14 Aug 1951, *E. Rouleau 2408* (MT, NFLD, DAO); Steady Brook, Humber River, 19 Aug 1948, *E. Rouleau 482* (MT, NY, NFLD, ACAD, CAN, DAO)] were examined by S. Galen Smith (WIS) in 1999 for the Flora of North America Project, and determined to be intermediates between *E. erythropoda* and *E. palustris* (L.) Roem & Schult. However, typical examples of *E. erythropoda* remained unknown from Newfoundland. The presence of the species is now confirmed by the specimen from a saltmarsh on the northeast coast. The species is found across North America, with the next nearest location being in New Brunswick (Smith et al. 2002).

**Scirpus pedicellatus* Fernald

SPECIMEN CITATIONS: CANADA. Newfoundland: Long Range Mountains, Upper Humber River, upstream from Reidville, [49°14′N, 57°22′W], 28 Aug 2000, *C. Hanel, L. Lavers & C. Wentzell CH 000828-13* (NFM, MT); Long Range Mountains, Upper Humber River, Reidville, [49°13′N, 57°23′W], 30 Aug 2000, *C. Hanel, L. Lavers & H. Mann CH 000830-2* (NFM, MT, Sir Wilfred Grenfell College).

These first Newfoundland collections of this eastern North American species were made by the NFRPP on the west coast of the Island. The plant grows on the muddy banks of backwaters of the Humber River. The identities of both collections were confirmed by Alfred E. Schuyler (PH). The next nearest records are from Nova Scotia (Whittemore and Schuyler 2002).

JUNCACEAE

Juncus subcaudatus (Engelm.) Coville & S. F. Blake

SPECIMEN CITATIONS: CANADA. Newfoundland: St. George's Bay, Fishells Brook, near mouth, [48°19′N, 58°42′W], 9 Sep 2000, *N. Djan-Chékar & C. Hanel NDC 00-1584* (NFM, MT); 10 Sep 2000, *N. Djan-Chékar & C. Hanel NDC 00-1627, NDC 00-1634, NDC 00-1636* (NFM, MT); Exploits Valley, Grand Falls, Exploits River, below (S of) dam, [48°55′N, 55°40′W], 28 Aug 2001, *C. Hanel, H. Thomas & J. Hancock CH 010828-34* (NFM, MT); Grand Falls, W of community, Thunder Brook, [48°56′N, 55°49′W], 30 Aug 2001, *C. Hanel & J. Hancock CH 010830-11* (NFM, MT).

This species was first reported for Newfoundland in 1990, following a revision of historical specimens that had been misidentified (Hay et al. 1990). On the basis of these records, the species was known only from the Avalon Peninsula [Peter's River, approx. 2 mi. southeast of, 17 Sep 1959, *E. Rouleau 5156* (MT, NFLD)], and from north central Newfoundland [Grand Falls, 11 Aug 1911, *M. L. Fernald, K. M. Wiegand & H. T. Darlington 5127* (MT, GH); Grand Falls, along the Exploits River, 12 Aug 1911, *M. L. Fernald, K. M. Wiegand & H. T. Darlington 5128* (GH); Sheffield Lake, Southwest Brook, at the mouth of, 16 Aug 1951, *E. Rouleau 2512* (MT, NFLD, DAO)]. The NFRPP found the species at Fischells Brook and in the Exploits Valley. The Fischells Brook collections extend the known range of the species into western Newfoundland.

POTAMOGETONACEAE

**Potamogeton richardsonii* (A. Benn.) Rydb.

SPECIMEN CITATIONS: CANADA. Newfoundland: Great Northern Peninsula, Indian Pond, 50°41′N, 57°13′W, 17 Jul 1997, *J. E. Maunder NFM 7700* (NFM); Grand Codroy River, NW of Doyles, 47°50′N, 59°12′W, 22 Jul 1997, *J. E. Maunder NFM 7701* (NFM).

Botanists from the NFRPP examined unidentified *Potamogeton* material held at NFM and discovered *P. richardsonii*, which was previously unknown for the Island. The specimens were collected at two

widely separated locations on the west coast of the Island: in a lake and in a slow-moving backwater of a large river. *Potamogeton richardsonii* is a North American endemic found across the continent (Haynes and Hellquist 2000). The next nearest records are from the Gaspé Peninsula, Québec (Faubert 2000), and Cape Breton Island, Nova Scotia (Zinck 1998).

**Potamogeton robbinsii* Oakes

SPECIMEN CITATIONS: CANADA. Newfoundland: Southern Long Range Mountains, Bottom Brook, E of Third Pond, [48°32′N, 58°12′W], 13 Sep 2000, *N. Djan-Chékar, C. Hanel, D. Brake & H. Smith NDC 00-1736* (NFM, MT); Exploits Valley, Grand Falls, W of community, Exploits River, [48°56′N, 55°45′W], 30 Aug 2001, *C. Hanel & J. Hancock CH 010830-43* (NFM, MT).

This species is patchily, but widely, distributed throughout North America (Haynes and Hellquist 2000). The collections reported here are from backwaters along rivers in two different watersheds, one on the west coast and one in central Newfoundland. The next nearest records are from Cape Breton Island, Nova Scotia (Zinck 1998).

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IN MEMORIAM

Richard Alden Howard
1917–2003

Two forces of nature hit Massachusetts in September 1938. The Great Hurricane swept through on the 22nd, dramatically altering New England's landscape. Richard Alden Howard arrived in Cambridge that same week to make his own, far more positive impact on Harvard's landscape, and later, on the 265 acres at the Arnold Arboretum in Jamaica Plain, Massachusetts.

Howard was born in Stamford, Connecticut, and reared in Warren, Ohio. He graduated from the Botany Department at Miami University in Ohio in 1938. Afterward, unable to afford graduate school, he accepted a position as a technician at Harvard University under Irving W. Bailey. Bailey put him to work on a little-known group of tropical flowering

plants, the Icacinaceae. Howard also attended classes, and in 1939 the Society of Fellows awarded him a Junior Fellowship that supported his postgraduate training. As a graduate student, he had the opportunity to visit Harvard's Atkins Garden at Soledad, near Cienfuegos, Cuba. The experience inspired both his life-long interest in tropical plants and his relationship with the scientists in the Caribbean. It was also where he met one of the great plant explorers, David Fairchild. After Cuba was restricted, Howard continued his tropical research and teaching efforts at the Fairchild Tropical Garden in Miami and visited Fairchild's estate, the "Kampong," in Coral Gables, Florida.

Howard continued the work he had started under Bailey on the Icacinaceae and completed his doctorate in 1942. His thesis, entitled "Studies of the Icacinaceae: A monograph of the New World species," was later published in a series of papers.

The country was at war. Howard wanted to enlist in the United States Navy, but he was rejected because his height of 6′5″ exceeded U.S. Navy limits. Instead, he entered the Army Air Corps where his combination of leadership, teaching skills, and practical knowledge of tropical plants led to his assignment with the newly established Research and Rescue Program of the Air Force. He was appointed its first director and devoted the rest of his time in service to teaching airmen how to survive in freezing snow, scorching sands, sweltering jungles, and adrift on desolate oceans. He wrote survival manuals (some published on edible paper and sized to fit inside a combat boot) that were published by the Arctic, Desert, Tropic Information Center (ADTIC). When he left the service, he was a captain, and he continued as a consultant to ADTIC for several years. The Air Force recognized his contributions by presenting him with the Legion of Merit in 1947. Howard continued not only to write, but also to collect survival manuals, and amassed a unique collection that he donated to Harvard's Houghton Library in 1998.

Following the war, Howard and his bride, Elizabeth "Betty" Solie, moved to New York where Howard worked as a curatorial assistant at the New York Botanical Garden. In 1948, he was called back to Harvard as an Assistant Professor responsible for the botanical semester of the large introductory biology course. He proved to be a popular and innovative lecturer, who often provided generous supplies of edible plants to demonstrate his belief that the best way to a student's mind was through his stomach. At the same time, he published papers on the floristics of the West Indies and New England.

In 1953, the University of Connecticut appointed Howard the Professor of Botany and Department Chair. His stay in Connecticut

was short-lived since he was recruited back to Harvard in 1954 as the Arnold Professor of Botany and Director of the Arnold Arboretum.

Howard's new challenge was to guide the Arnold Arboretum through a period of tremendous change and turmoil. Controversy surrounded Harvard's decision to move portions of the Arboretum's herbarium and library from Jamaica Plain to a new facility in Cambridge. Despite an atmosphere charged with tension, Howard forged ahead. He possessed the stamina, integrity, and sense of humor to carry him through a contentious decade. Critics were won over by his zealous promotion of the Arnold Arboretum and all things botanical and horticultural. He gave countless lectures at garden clubs and cultural organizations and presented his lecture, "A Botanist in Your Grocery Store" more times than he could recall. Among his other favorite talks were "Botany in Boston Restaurants," "Jungle Housekeeping," and "South to the Antilles." He was in such demand that he often joked about "living out of a suitcase for weeks on end," but he knew that he was rebuilding a support network, and he channeled all of the honoraria back into the Arboretum's public education programs.

Howard encouraged the Arnold Arboretum staff to become active in local, national, and international botanical and horticultural organizations. He and staff members were soon involved in the Horticultural Club of Boston, the Massachusetts Horticultural Society, the New England Botanical Club, the American Association of Botanical Gardens and Arboreta, the American Society of Plant Taxonomists, the Botanical Society of America, the International Association of Botanical Gardens, and the International Society of Plant Taxonomists. Howard served as an officer for many of these organizations. He also encouraged the library staff to join the newly organized Council on Botanical and Horticultural Libraries when it held its first meeting in Boston in 1968.

During his twenty-four years as Director, Howard assembled a capable team to advance the mission of the Arnold Arboretum. He was interested in every aspect of the operation and made himself available to his staff when decisions were needed. He acknowledged both personal and professional achievements and milestones of the staff and volunteers in the *Arboretum Newsletter* and in his annual *Director's Reports*. He restored the botanical and horticultural reputation of the institution, improved the grounds, and built greenhouses. While cultivating mutually beneficial relationships with the City of Boston and its Parks Department, he nevertheless thwarted attempts by the city to reclaim portions of the Arboretum for other purposes. Computerization of botanical records was in its infancy, and Howard was among

the first to introduce this new record-keeping system to the Arboretum. He bolstered the Arboretum's public education program, introduced innovative uses for the Arboretum's Case Estates in Weston, Massachusetts, and promoted major research projects like the Generic Flora of the Southeastern United States in the *Journal of the Arnold Arboretum*. Howard shuttled from his home at the Case Estates to Jamaica Plain and then on to Cambridge nearly every day for almost twenty-four years. He maintained two offices and supervised staff on both sides of the river. His motivation was clear, his energy boundless. He considered his success at the Arnold Arboretum to be his greatest professional achievement.

Howard was not content to limit the Arnold Arboretum research program to his sphere of interests. In the early 1970s he took every opportunity to rebuild relations with botanical institutions in China. By the mid-1970s he succeeded in renewing the exchange of specimens, and he was able to visit colleagues in 1978 as a member of the Botanical Society of America's delegation. In 1980 the Arnold Arboretum resumed its botanical interests in China by sending a new team of botanical explorers, and hosted a stream of Chinese botanists in Cambridge to collaborate on the Flora of China project.

Professor Howard continued to teach in Cambridge and lead Harvard students on field trips to Cuba until the formal relationship with the Garden ceased in 1961. From then on, although field studies were conducted in the Everglades and elsewhere in subtropical Florida, he continued to correspond and exchange materials with his Cuban colleagues.

Howard devoted more time to collecting on islands throughout the Caribbean, frequently traveling with colleagues and family members. He joked about his wisdom in choosing to explore the tropics, but the work was often dangerous. He and his team worked in remote locales, trekked over rough terrain, and scaled slick volcanic mountainsides.

Howard's extensive knowledge of tropical vegetation was put to practical use. Aluminum companies sought his help in the revegetation of strip-mining sites in Jamaica, and later in Hawaii. A grant received from the National Science Foundation permitted him to study the montane elfin forests at Pico del Oeste in the Luquillo Mountains of eastern Puerto Rico, a project that resulted in 17 related papers. The Boston Poison Information Center relied on his advice on the poisonous properties of plants, and he was "on call" to them for many years.

The work that represents the culmination of Howard's research in the West Indies is the six-volume *Flora of the Lesser Antilles* (1974–1989).

In the foreword to *Volume 1*, Howard wrote, "Since the time of the voyages of Columbus much botanical data has [sic] been assembled from the various islands of the Lesser Antilles. Yet, after almost five hundred years, a unified and comprehensive account of the specific components of the vegetation that flourishes on that chain of islands is still wanting. The launching of the publication . . . is aimed to fill this gap just before the last steadfasts of our natural vegetation succumb to the recklessness of man and his civilization. . . .The undertaking of the preparation of a definitive flora dates back to some twenty years involving both extensive field work, combined with exploration, and intensive research in herbaria." The series was completed in 1989 and it is still a standard reference work on Lesser Antilles flora.

Professor Howard asked to be relieved of his administrative duties in 1978. He continued his teaching and research as Professor of Dendrology in Cambridge. His courses ranged from introductory botany to graduate level classes in the phylogeny of flowering plant families and advanced plant anatomy, and he was proud to have supervised three graduate students. In 1988 when he reached mandatory retirement age, he taught his last course at Harvard: "Plants and Human Affairs." He was asked to substitute at the last minute, but did not hesitate to accept since it was a course that he had always wanted to teach. His research during this period focused on his extensive survey of the nodal and petiolar structure of the vascular conducting system through which plants move materials between leaf blade and stem. Howard left Cambridge briefly from July 1989 until September 1990 to serve as the Vice President for Science at the New York Botanical Garden.

Richard Howard was an international good-will ambassador for the botanical and horticultural sciences. In 1963 he made a world tour, visiting gardens and herbaria at every stop, collecting whenever he could, and taking pictures of plants and people to add to his already voluminous collection of Kodachrome slides. He served on boards and consulted at established or new botanical and horticultural organizations like the Pacific Tropical Garden based in Kauai, Hawaii (now the National Tropical Botanical Garden), the Acton (Massachusetts) Arboretum, the Coastal Maine Botanical Garden, the Fairchild Botanical Garden, and at the beloved Kampong. He was thrilled to return to Cuba and the garden at Soledad in 1999 with a delegation sponsored by Harvard's David Rockefeller Center for Latin American Studies. In a surprise finale to the conference, the Cuban delegation planted two new palm trees in his honor.

Over a 60-year period Howard published 13 books and more than 300 papers. The depth and breadth reflect his eclectic interests. He wrote on plant anatomy and morphology, floristics, cultivated plants, economic botany, tropical ecology, biogeography, the social and economic history of the West Indies, biographical profiles of botanists, and botanical trivia. Even in his later years when his eyesight and general health began to fail him, he spent his good days working in the library on various projects and manuscripts.

During his long career Howard received many awards. The Jamaica Natural History Society, the Montserrat Natural History Society, and the Montserrat National Trust acknowledged his botanical contributions to their islands. The American Association of Botanical Gardens and Arboreta, the American Herb Society, the American Horticultural Society, the Garden Club of America, the City of Boston, the Massachusetts Horticultural Society, and the National Council of State Gardens bestowed horticultural awards upon him. He was named an honorary fellow of the Danish Royal Academy of Arts and Sciences, and received the Distinguished Citizen Award from his hometown of Warren, Ohio. He was awarded an honorary Doctor of Science at Framingham State University in 1977. The National Tropical Botanical Garden named him the 1999 recipient of the Allerton Award in recognition of his decades of service in the advancement of tropical horticulture and the understanding of tropical plants.

Howard was a member of the New England Botanical Club from 1940 until his death. He served as president in 1953 and held the record as the most often featured speaker at the Club's milestone meetings—the 700th, the 800th, and the Centennial. At the Centennial meeting, Howard was not content merely to summarize the highlights of 100 years of the organization. He commissioned noted author, Maurice Sagoff, to compose a poem about the NEBC that he read at the end of his speech.

The Howards reared four children, Jean, Barbara, Bruce, and Philip, and the family shared many botanical adventures. Betty co-authored several papers with her husband and edited many more. She co-hosted open houses, exotic botanical-theme dinner parties, international dignitaries, impoverished students, and prospective faculty and staff. She was a true partner in life, traveling the world with him, and managing their family and home when he was off on his own. They were proud of their children and eight grandchildren, and in later years, looked forward to annual family reunions in Florida. Of course, Howard timed them to coincide with his work on the inventory of plants at the Kampong.

Richard Alden Howard's legacy to Harvard and the fields of botany and horticulture are as large as his life. The citation presented to him by Framingham State College in 1977 is an apt tribute. It reads "Scholar, interpreter of the world of plants to people of all ages, botanical explorer of the world's remote corners, entrusted with the care of our botanical treasures, he has taught us survival in the wilderness and the beauty of civilized nature."

ACKNOWLEDGMENTS. Special thanks are due to Bruce Howard and staff of the Arnold Arboretum and the Harvard University Herbaria for contributions and corrections.

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—JUDITH A. WARNEMENT AND CARROLL E. WOOD, JR., Harvard University Herbaria, Cambridge, MA 02138.

RHODORA, Vol. 106, No. 926, pp. 185–187, 2004

BOOK REVIEW

Manual of Vascular Plants of Northeastern United States and Adjacent Canada, Second Edition by Henry A. Gleason and Arthur Cronquist. 1991 (seventh printing, 2004). xlvi + 993 pp. ISBN 0-89327-365-1 $69.00 (hardcover). The New York Botanical Garden Press, Bronx, NY.

My e-mail read: "Just wondering—why do you want the book reviewed when the second edition has been out for years?" The reason is that this wonderful book, now in its seventh printing, has several new and useful features that will make it worth your buying a copy. Most noticeably: the cover has changed, corrections have been made in the text, the indexes have been expanded, and there are now photographs and short biographies of Gleason and Cronquist included in the volume.

The first thing you'll notice is the new cover. The bright green, slightly flexible, hard cover has been replaced by a stiffer cover that is darker green and illustrated with an impression of a beautiful drawing of *Liriodendron tulipifera* by Bobbi Angell. Inside the front cover there is still the helpful outline map of the 48 contiguous states with the shaded portion representing the coverage of the *Manual*. A very useful feature printed inside the back cover is a ruler, something we at UNH have been having students tape into their books for years. The *Manual* dimensions have been increased slightly while retaining the pagination of previous printings; thus, the page numbers still match those in the *Illustrated Companion*.

There have been several positive changes made in the front matter. First, there is now a table of contents, which will be very helpful for locating a family quickly. Of course, you can still find the page number for a family by scanning the expanded index section. Second, there is a foreword written by the Holmgrens describing the changes made to the *Manual* and asking for corrections for future editions. Third, Noel Holmgren has contributed short biographies of Henry Allan Gleason and Arthur Cronquist—a delight for all of us who love history as well as systematics. The photos are classics, too: Dr. Gleason with an armload of folders of herbarium specimens, and Dr. Cronquist in his office with his feet up on the table, absorbed in a book and surrounded by books and specimens. Fourth, a short floristic summary has been added to the page with frequently used abbreviations. Fifth, the listing of "more frequently cited botanical authors" has been left out of this printing. I suppose it was difficult to keep this list to a manageable size, and those abbreviations can be found elsewhere, but I am sad to see it gone because I like to think that

students in systematics classes found it helpful and interesting. Sixth, the glossary has been moved to follow the text.

Although the new printing is not a revision of the text of the second edition, it does incorporate some corrections in nomenclature suggested by members of the botanical community. In addition, in some cases nomenclature has been changed to agree with that in published volumes of *Flora of North America North of Mexico* and synonyms have been added. Author abbreviations have been standardized to agree with Brummitt and Powell's *Authors of Plant Names*. A very helpful change, I think, is that now a period follows only those names that are abbreviated; several spaces set off the common name from the scientific name and the description. Miscellaneous errors have also been corrected during proofreading. The very useable keys and thorough descriptions we are familiar with from previous printings constitute the bulk of the volume.

The back matter has been changed considerably in this printing, and now includes the glossary and an expanded index section. A couple of style changes to note in the glossary are that there is no longer a wide space setting off the term from its definition (I'm sorry to see that gone because I found it helpful, visually), and there is now a blank line to indicate the transition to the next letter in the alphabetical listing of terms. The terms are still easy to pick out in the list because of the boldface type. A big change in the new printing of the *Manual* is the revised and expanded indexing, contributed by Neil Harriman. In this volume, common and scientific names have been put into separate indexes, which will be kind of frustrating for me since I frequently find myself drifting into a search of the wrong list in other books with separate indexes (the down side of being bilingual with respect to plant names). As a benefit, more entries are offered in each index. In the index to scientific names, all infraspecific taxa have been listed, not just those in selected genera. Synonyms and taxa casually mentioned in the text are listed as well, and are set apart by being in italic type. In the separate index to common names, a much more detailed listing is provided than in previous printings with the combined index. The result is an index section that is almost double the number of pages than in previous printings, and which should prove to be extremely useful. The last change to this section of the book is that there are no longer blank pages available for notes.

The final page of this new printing of Gleason and Cronquist's *Manual of Vascular Plants* has a photo of Arthur Cronquist's back as he walks off into the woods, a book held behind him. My favorite since published in its second edition—the very useable and now corrected and

expanded *Manual*—will continue to be my choice in the field as well as at the microscope.

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BOOK REVIEW

Flora of the Hudson Bay Lowland and its Postglacial Origins by John L. Riley. 2003. viii + 236 pp. maps, color plates. ISBN 0-660-18941-0 US$49.95 (softcover). National Research Council Research Press, Ottawa, Ontario, Canada.

This book is the culmination of three decades' worth of floristic research conducted in the Hudson Bay Lowland, one of the last regions in North America to have its flora and vegetation documented. John L. Riley, Director of Science and Stewardship for the Nature Conservancy of Canada, has masterfully integrated new floristic data with previous botanical studies to provide a comprehensive catalogue of the Lowland's unique vascular plants. Floristic analysis is approached with regard to coincident distribution patterns within and beyond the region, and follows with a discussion of the groups of taxa that share similar postglacial origins.

In addition to the Abstract (both in English and in French) and Introduction, the book includes sections on methodology, results—regarding distribution patterns and floristic zonation, "Postglacial Origins of the Flora," and a Conclusion. The flora includes numerous maps pertaining to glacial history, vegetation zones, and species distribution. Thirty-two color plates illuminate the geological and hydrological features of the Lowland landscape, some of the plant communities that occur there, and several of its native species. Each plate is accompanied by a brief description of distribution and/or habit.

In his Introduction, Riley provides a wonderful account of the geology and glacial history of the Hudson Bay Lowland. One of the most intriguing facts regarding the Lowland is its relatively recent colonization by terrestrial flora and fauna. This region's location is close to the center of the Laurentide Ice Sheet, a massive lobe of ice covering much of northeastern North America during the late Wisconsin Glaciation. Consequently, the Lowland has experienced isostatic rebound, and in some locations has provided widths of 30 km of newly colonizable landscape in the last millennium. Attributes unique to this landscape are also discussed, including glacial features, hydrology, soils, permafrost, peatlands, and the role of climate and climate change.

A brief literature review reflects on previous research conducted in the Hudson Bay Lowland. Existing maps of geographic, vegetation, and climatic zones as illustrated in the text have provided the basis for the author's stratification of 11 data-collection areas. The systematic

treatment includes 816 native species (857 geographically and ecologically distinct taxa) and 98 non-native species. Species are arranged according to the order of families in Dalla Torre (1958) and Verdoorn (1938), with genera and species organized alphabetically by scientific name within each family. Synonyms and common names are also provided. The catalogue of Lowland species, provided in Appendix B, includes occurrence status of each species with regard to each data collection area, continental distribution, and the distribution and frequency of taxa within the Lowland. These data are provided in a coded format with an accompanying key. After some familiarization with the key, I found the codes relatively easy to use. In addition, excluded taxa are also noted, each with an accompanying reason for their exclusion. These records are found in Appendix C.

Discussion and interpretation of the geographic affinities of the native taxa, coincident distribution patterns, and floristic zonation descriptively illustrate the character of the Lowland flora. The simple black-and-white distribution maps found in Appendix A are a major component of the book. These illustrate 148 of the species in the Lowland, combining dot-distribution and range-limit maps to provide precise species distributional data within the broader distributional patterns. Literature sources for these maps are indicated on the legend of each map.

The section on "Postglacial Origins of the Flora" includes information on the geological strata, plant migration, and vegetation development. A historical account of the late-Wisconsin glaciation elegantly describes the consequences of glacial melting on regional and continental events. Several maps illustrate the approximate position of the ice sheet during de-glaciation. Riley includes data from paleobotanical research to assist in the interpretation of migration and vegetation patterns following the de-glaciation and rebounding of the Lowland landscape. A follow-up of non-native introductions and rare species concludes this section.

For those who are interested in natural history and phytogeography, you will find this book to be an invaluable resource. Although not meant to be used as a field guide, this book will serve as an excellent reference and accompaniment to other literature covering the flora and geology of Canada and the northeastern United States.

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NEW BOOKS

Common and Occasional Bryophytes of the Virginia Piedmont by David Breil. 2003. illus. $10.00 (softcover). Published as *Banisteria* #21 by the Virginia Natural History Society, Box 62, Hampden-Sydney, VA.

Flora of North America North of Mexico, Volume 4: Magnoliophyta: Caryophyllidae, Part 1 by Flora of North America Editorial Committee, eds. 2004. xxiv + 559 pp. line drawings, distribution maps. ISBN 0-19-517389-9 $120.00 (hardcover). Oxford University Press, New York and Oxford. [www.oup.com]

Forests in Time: The Environmental Consequences of 1,000 Years of Change in New England by David R. Foster and John D. Aber, eds. 2004. 496 pp. 202 illus. ISBN 0-300-09235-0 $45.00 (hardcover). Yale University Press, New London, CT. [This title can be ordered directly from Harvard Forest, P.O. Box 68, Petersham, MA 01366; send a check for $30.00, payable to Harvard University.]

Manual of Vascular Plants of Northeastern United States and Adjacent Canada, Second Edition by Henry A. Gleason and Arthur Cronquist. 1991 (seventh printing, 2004). xlvi + 993 pp. ISBN 0-89327-365-1 $69.00 (hardcover). The New York Botanical Garden Press, Bronx, NY.

A Primer of Ecological Statistics by Nicholas J. Gotelli and Aaron M. Ellison. 2004. xviii + 510 pp. illus. ISBN 0-87893-269-0 $34.95 (softcover). Sinauer Associates, Inc., Sunderland, MA.

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NEBC MEETING NEWS

January 2004. The night's meeting, being the "Fourth Foray into Food and Flowers," began with a potluck dinner featuring many dishes with a botanical theme. Some of the notable contributions this year included pickled *Salicornia* (glasswort), vegetarian chili, and other spicy dishes to warm us up on a bitterly cold night. There were also several desserts featuring the ever-popular *Theobroma cacao* (chocolate). Once members could tear themselves away from the food, they perused books and other items for sale, or bought tickets for the raffle of botanical books.

Following the feast, members settled into their chairs for a night of "show and tell." Each person was allowed ten slides, or ten minutes, to show the club interesting botanical exploits from the past year. Don Lubin started the night with a digital slide show of pteridophytes (ferns and fern allies), including species from Bermuda and Mt. Washington. Members who wanted a closer look were invited to visit Don's website [http://www.theworld.com/~donlubin].

The "true" slide show then began, with President Paul Somers showing photos of the Southern Appalachians, a thinly veiled plot to encourage members to sign up for the club trip to that region this May. Bryan Hamlin was next with brilliant macro shots of orchid species and *Gaultheria hispidula* (creeping snowberry). George Newman followed with his photos from Burnt Cape. This ecological reserve in Newfoundland, visited by Fernald, featured the dwarf-like willow species *Salix uva-ursi* (bearberry willow) and *Salix vestita* (rock willow). Alice Schori then presented her slides of NEBC members in the act of botanizing at several New England locations. She was followed by Marsha Salett, whose slides of Cape Cod, from her recent photography exhibition "From Bogs to Beaches," brought many "oohs" and "aahs" from the crowd.

Following Marsha, it was back to the computers. After Bryan snuck in a few more photos of ericads from his digital collection, Corresponding Secretary Nancy Eyster-Smith tapped into her own huge digital image collection, wowing the audience with a photo of a rest-stop *Pimpinella anisum* plant (anise), from her family trip to Florida. The "show and tell" ended with Jennifer Forman Orth's images of "botanical oddities," including a variegated *Celastrus orbiculatus* (Asiatic bittersweet) and the invasive orchid *Epipactis helleborine* (broad-leaved helleborine). When the lights came back up, members retired to the refreshments room to hear the winning numbers for the book raffle, and perhaps for a second helping of dessert.

March 2004. Les Mehrhoff introduced the night's speaker, Dr. Bernard Goffinet from the University of Connecticut. His talk was entitled "When a phenotype belongs to multiple genotypes: Phylogenetic affinities of North American species in the lichen genus *Dendriscocaulon*." Lichens are a symbiotic association between a fungus (the mycobiont) and populations of unicellular or filamentous algae or cyanobacteria (the photobiont). This association tends to be stable, and also obligatory for the fungus, while some species of photobionts can be free-living. Dr. Goffinet compared the fungus-algae association to that of an agricultural system, with the fungus depending on the output of the algal "crops." The morphology of fungus species that lichenize is very different when the fungus is grown alone in culture and resembles callus tissue.

There has been much research focused on species specificity in lichen relationships. Some fungus species have a high degree of specificity, such as *Diploschistes muscorum*, which will appropriate *Trebouxia showmanii*, the photobiont of the lichen *Cladonia*, to establish independent thalli. Yet in some cases, two or more species of algae have been isolated from a single lichen, indicating that if there is specificity, it is not narrow. Researchers in Finland coined the term "lichen guilds" to refer to groups of fungi that share related photobionts. For example, many epiphytic lichens form a guild that shares the same cyanobacterial strain. The photobionts differ from those of terrestrial lichens, even when the mycobionts of the epiphytic and terrestrial lichens are congeners.

About 90% of lichens are associations between fungi and green algae, while 10% are fungi and cyanobacteria (blue-green algae). Some fungi have a primary association with a green alga as well as internal or external warts of cyanobacterial colonies known as cephalodia. These tripartite relationships can change, as occurs with *Peltigera leucophlebia*, which first adopts cyanobacteria following reproduction via fungal spores, then forms a macrothallus with green algae, and finally forms cephalodia. *Sticta felix* lichenizes with cyanobacteria in some locations, but forms a morph with green algae in drier, high-light habitats. Recent molecular research has revealed several cases where what appeared to be two different lichen species were actually the same fungus associating with two different photobionts. *Lobaria amplissima*, for example, forms a foliose (flat) lichen when associating with a green alga, and a fruticose (branched, treelike) lichen with a cyanobacterium. The lichen once identified as *Nephroma silvae-veteris* was discovered through molecular and chemical testing to be a foliose cyanomorph of *Lobaria oregana*.

Bernard then spoke about his research, asking the question: have the many fungi that lichenize into "Dendriscocauloid" growth forms (lichens in the genus *Dendriscocaulon*) evolved from a single ancestor, or do they represent a polyphyletic group? In North America two species of *Dendriscocaulon* have been identified. These species likely represent cyanomorphs of lichens involving a green alga. The question is, which species? Using the ribosomal DNA sequences of the ITS, he compared 110 lichen samples (about 25 haplotypes) assigned to several different genera. When the sequences were aligned, there were some conserved regions, but also significant amounts of variation. Looking at only the conserved regions of the DNA, he could separate the samples of North American *Dendriscocaulon* into at least four fungal lineages, indicating that these *Dendriscocaulon* thalli share their fungus with either 1) *Sticta wrightii*, 2) *Lobaria quercizans*, 3) *L. amplissima*, or 4) some yet unidentified lineage.

Dr. Goffinet then turned to an examination of the photobiont genus *Nostoc*, a strain of cyanobacteria. Only one strain of *Nostoc* is found per lichen, with some fungus species like *Peltigera aphthosa* exhibiting a high degree of specificity. The *Nostoc* found in the cephalodia of a lichen formed with green algae is different from that found in a free-living cyanomorph (simple fungus-cyanobacteria association). Sequencing of *Nostoc* of Dendriscocauloid lichens has yet to show a taxonomic or geographic pattern.

April 2004. Vice President Karen Searcy introduced the night's speaker: Julie Dragon, a Ph.D. candidate at the University of Vermont. Julie, who received the club's Graduate Student Award in 2003, spoke about "*Carex lenticularis* and its allies: Phylogeny, biogeography, and species delimitation."

Carex is a cosmopolitan genus of approximately 2500 species of sedges. When Julie first became interested in the genus, she spoke with Lisa Standley, past NEBC President and resident *Carex* expert. Lisa recommended exploring the *C. acuta* complex, 12 species in section *Phacocystis*, with a chromosome range of 42 to 46. For her Master's thesis, Julie investigated the cohesiveness of the *C. acuta* complex and its possible sister complexes. She began by collecting samples of all of the species in the complex, along with other species in section *Phacocystis*, and some from sections with a putative sister affiliation. The species she collected came from many locations, including Vermont (*C. lenticularis*) and Quebec (*C. paleacea*). She also received samples from places as diverse as Washington state (*C. lenticularis* var. *lipocarpa*), Iceland (*C. nigra*, *C. rufina*, *C. bicolor*), Argentina (*C. decidua*), and Denmark (*C. trinervis*).

Julie sequenced DNA from each sample, focusing on two ribosomal DNA spacers: ITS and ETS. With strict consensus of two parsimonious trees, she found that *Carex torta*, *C. gynandra*, and *C. crinita* were separated from the rest of the taxa by *C. podocarpa* of section *Scitae*, indicating that section *Phacocystis* is polyphyletic. The data further revealed that the *C. acuta* complex was not a natural complex, but rather consisted of two groups, with major taxa between them. Further support for the clades identified by the data included geographic cohesiveness, with species grouping according to their native ranges: Eurasia, Austral Asia, and America.

For her Ph.D. research, Julie is looking more closely at the American clade, which includes *Carex lenticularis* and its allies, and *C. aquatilis*. While *C. aquatilis* is monophyletic, *C. lenticularis* is not, with its western varieties sister to *C. aquatilis* and its eastern varieties sister to the amphi-Atlantic *C. rufina* and South American *C. decidua*. She has completed additional sampling within the clade and will be adding chloroplast DNA sequences to the molecular analysis. Sedges from Mexico (*C. hermannii*), the western U.S. (*C. lenticularis* var. *dolia* and var. *impressa*), and Alaska (*C. utriculata*, *C. microchaeta*, and *C. mertensii*) were collected for this portion of her research. Julie noted that during her field season in Alaska, her most remarkable find may have been *C. lenticularis* var. *dolia*, a rare species she happened upon along a roadside.

Julie then constructed a new phylogenetic tree that included the new samples from Alaska along with the rest of the American clade and outgroup taxa. Preliminary analysis indicates that the Alaskan species *Carex spectabilis* and *C. podocarpa*, which are placed together in section *Scitae*, are part of a single clade. However, another member of the same section, *C. microchaeta*, is sister to *C. aquatilis*. While much of the topology of the tree remains the same, samples of *C. lenticularis* var. *dolia* (Montana) and *C. eleusinoides* (Siberia) remain part of an Austral-East Asian clade, separate from the same taxa and other varieties of *C. lenticularis* in the American clade. Samples of *Carex bigelowii*, collected from both Alaska and Vermont, formed a clade, but were separated by *C. scopulorum*, a species native to the northwestern U.S. Her future research will include using the molecular phylogeny to reexamine the morphology of the *C. lenticularis* group, determining what morphological characteristics reflect the evolutionary history of the clade, and revising the taxonomy as necessary.

—Jennifer Forman Orth, Recording Secretary.

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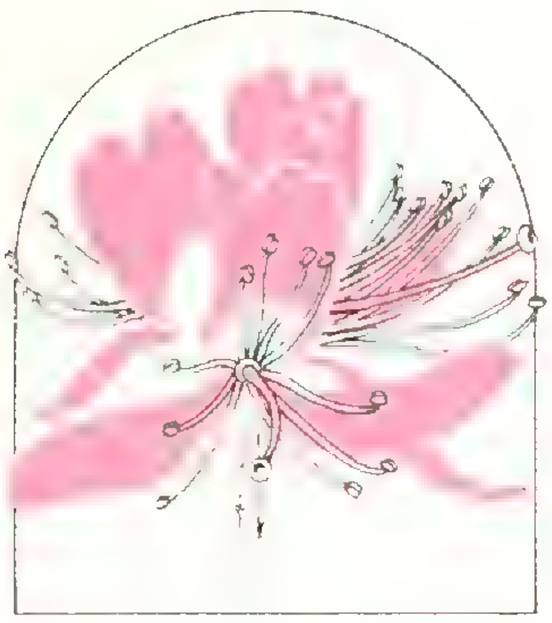

RHODORA

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New England Botanical Club

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FOSSIL *NEVIUSIA* LEAVES (ROSACEAE: KERRIEAE) FROM THE LOWER-MIDDLE EOCENE OF SOUTHERN BRITISH COLUMBIA

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ABSTRACT. Fossil leaves assigned to the disjunct rosaceous genus *Neviusia* A. Gray, *N. dunthornei* DeVore, Moore, Pigg & Wehr *sp. nov.* (Rosaceae, tribe Kerrieae) are described from the lower-middle Eocene One Mile Creek locality near the town of Princeton, southern British Columbia, Canada. The leaves are elliptic to broadly ovate, seven-lobed, up to 4.9 cm long × 5.6 cm wide with craspedodromous venation and two to three sizes of marginal teeth. They bear a striking resemblance to *N. cliftonii* Shevock, Ertter & Taylor, the recently discovered species of the Mount Shasta area of northern California, and differ markedly from the type species *N. alabamensis* A. Gray of southeastern North America. The occurrence in the Okanogan Highlands of *N. dunthornei* marks the first fossil evidence for the small, rosaceous tribe Kerrieae, and further documents the lower-middle Eocene as a time of major radiation of many temperate families, including the Rosaceae.

Key Words: biogeography, Eocene, fossil leaf, Kerrieae, *Neviusia*, Rosaceae

Neviusia A. Gray (Rosaceae, tribe Kerrieae; Snow Wreath) is a small genus of flowering shrubs consisting of two extant species, *N. alabamensis* A. Gray of southeastern North America and *N. cliftonii* Shevock, Ertter & Taylor, from the Mount Shasta area of northern California. *Neviusia alabamensis* was first described from Tuscaloosa County, Alabama by Asa Gray in 1859 (Gray 1859; Small 1972). Features of this genus include shrubs with numerous apetalous flowers that bear

†Wes Wehr died of a heart attack on April 12, 2004.

five white, toothed sepals that extend beyond a flattened hypanthium. The flowers have numerous stamens with conspicuous white filaments and 2–4 pubescent carpels, each with a single pedulous ovule, that mature into drupe-like achenes (Small 1972). The type species, *N. alabamensis*, occurs in the southeastern United States and prefers limestone to shaley cliffs. It is known in a variety of such sites today roughly corresponding with the Mississippi Embayment (Coile 1988; Horn and Somers 1981; Long 1989; Moore 1954).

Neviusia has been placed in the small tribe Kerrieae along with the Asian genera *Kerria* DC. (Japanese Rose) and *Rhodotypos* Siebold & Zucc. (Jet Bead; Ertter and Shevock 1993). Features of the Kerrieae include persistent sepals that are either serrate or imbricate and 1–8 drupe-like achenes (Baillon 1869). The tribe was traditionally considered to be intermediate between Spiraeoideae and Rosoideae, two of the traditional four subfamilies of Rosaceae, on the basis of morphological features (Robertson 1974). In contrast to this classification, recent molecular phylogenies support the recognition of two major clades within the Rosaceae that include part of the family (Rosoideae *sensu stricto* and Maloideae *sensu lato*) plus several smaller groups, many at the tribal level, including the tribe Kerrieae. In phylogenetic analyses, relationships among these groups are not well resolved (Judd et al. 2002; Morgan et al. 1994). The tribe Kerrieae nevertheless is always represented as a distinct clade in these analyses and all recognized members of the tribe consistently form a monophyletic clade within large analyses of Rosaceae.

For some time this unusual tribe was noted as an example of the southeastern North American/Asian disjunct distribution recognized for many other angiosperm genera such as *Magnolia*, *Liquidambar*, and *Hamamelis* (e.g., Graham 1999; Li 1952, 1972; Tiffney 1985; Wen 1998). In 1992, a second species of *Neviusia* was discovered, surprisingly, in a remote area of the Mount Shasta region of northern California (Taylor 1993). This second species, *N. cliftonii* (Shasta Snow Wreath), is distinct from the type species *N. alabamensis* in both floral and vegetative characters (Faber 1997; Shevock et al. 1992). In contrast to the apetalous *N. alabamensis*, *N. cliftonii* has white oblanceolate petals, about half as many stamens (50 compared to around 100), shorter sepals and styles, and leaves that are more ovate to cordiform with coarser teeth. Like its southeastern counterpart, Shasta Snow Wreath also grows on limestone substrate, preferring cool canyons near creeks (Shevock et al. 1992).

The occurrence of *Neviusia* at Mount Shasta, California is initially perplexing. However, whereas many closely related disjunct taxa occur

today in the Tertiary refugia of eastern North America and eastern Asia, a number of plants with disjunct distributions can also be cited for northern California and Asia Minor. Examples include such genera as *Dirca* L. (Thymelaeaceae; Leatherwood), and *Calycanthus* L. (Calycanthaceae; Spicebush; Ertter 1993). During the time of the discovery of *N. cliftonii*, fossil floras of the Okanogan Highlands were beginning to provide considerable new information about the diverse lower-middle Eocene vegetation of the Pacific Northwest (Crane and Stockey 1987; Wolfe and Wehr 1987, 1988). These temperate floras, particularly in the localities near Princeton, British Columbia and Republic, Washington, may document the first major radiation of a number of temperate families including the Rosaceae (Wehr and Hopkins 1994), Betulaceae (Crane 1989; Crane and Stockey 1987; Pigg et al. 2003), and the *Acer*-like members of the Sapindaceae (Judd et al. 2002; Wolfe and Tanai 1987).

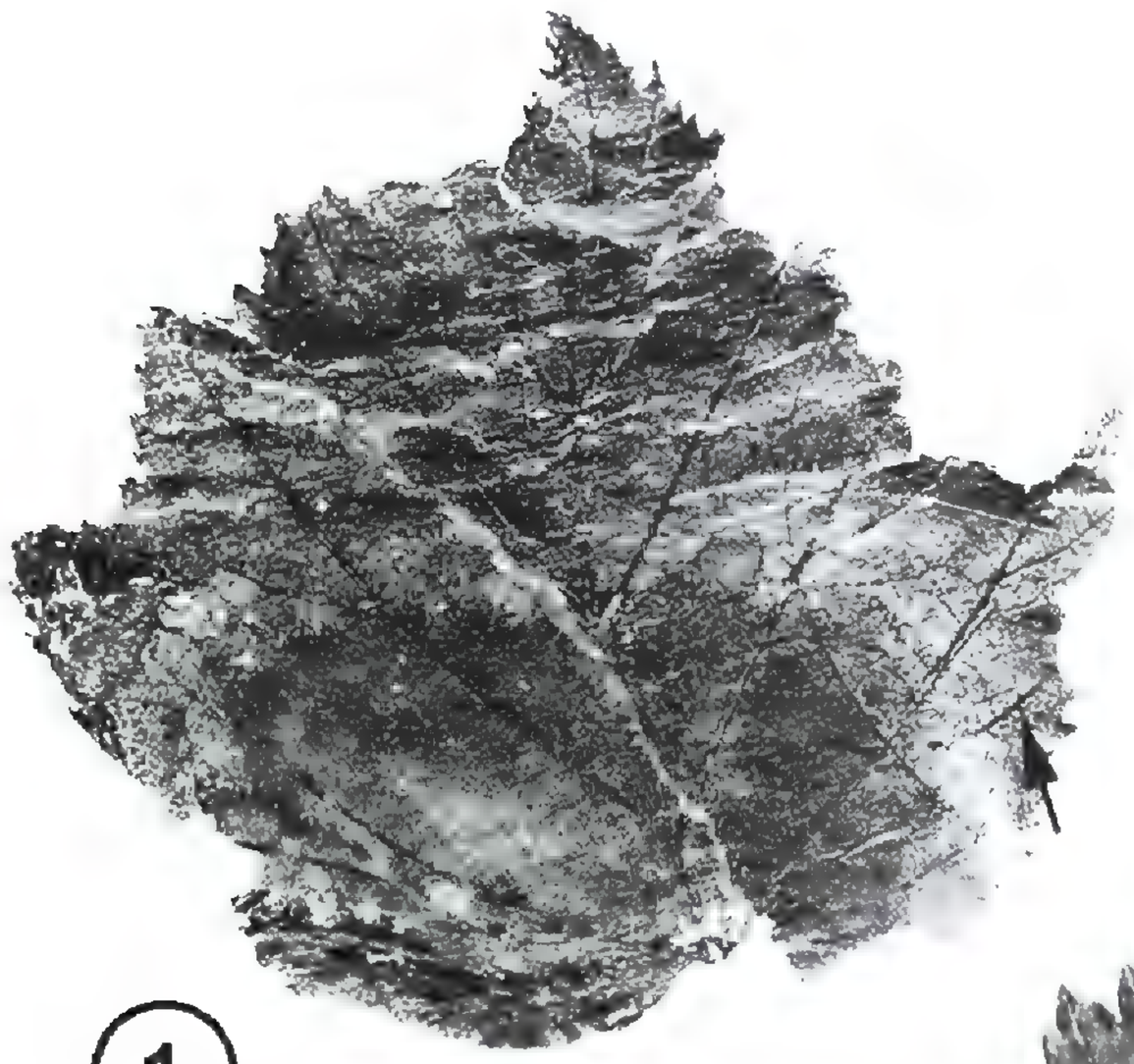
Fossil rosaceous leaves recognized from the Okanogan Highlands floras include both rare and commonly occurring representatives of extant genera from all four traditional subfamilies, as well as several extinct rosaceous forms. Among the genera represented are the rare examples of *Malus*/*Pyrus*, *Rubus*, and *Amelanchier*, the more commonly occurring *Prunus*, *Spiraea*, and *Crataegus*, and the extinct *Stonebergia* (Moore et al. 2002; Wehr and Hopkins 1994; Wolfe and Wehr 1987, 1988; W. Wehr, unpubl. data). Several specimens that were morphologically similar to the genus *Neviusia* were recognized at the One Mile Creek locality near Princeton, British Columbia and in the Republic flora of eastern Washington state (Wehr 1994; Wehr and Hopkins 1994). Of these, two specimens from One Mile Creek can now be assigned with confidence to *Neviusia*, while the others from Republic lacked diagnostic features and, although rosaceous, are of uncertain affinity. These fossil *Neviusia* leaves have been discussed by several authors (Ertter 1993; Shevock 1993; Stebbins 1993) and are occasionally mentioned in regional floras in connection with living *Neviusia* from California (sometimes inaccurately; e.g., Stuart and Sawyer 2001), but they have never been formally described. In the present contribution we establish the species *N. dunthornei* DeVore, Moore, Pigg & Wehr *sp. nov.* from One Mile Creek, near Princeton, British Columbia, Canada and document its relationship to the two known extant species of *Neviusia*. This fossil occurrence demonstrates the presence of fossil Kerrieae in western North America during the lower-middle Eocene, and figures significantly in our understanding of the phytogeography and early evolution of the rose family during its major Paleogene diversification.

MATERIALS AND METHODS

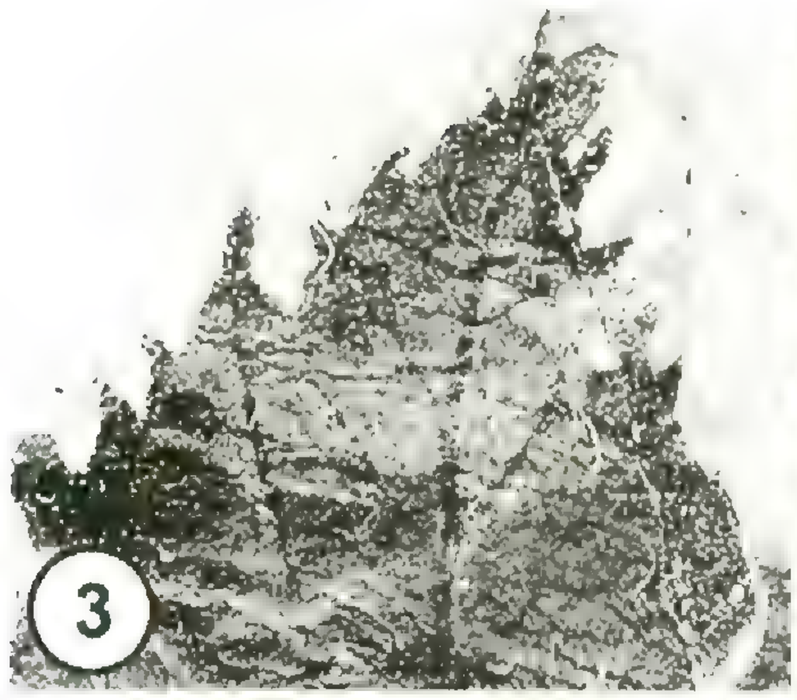
Specimens were collected from the One Mile Creek locality (also known as Allison Creek), in the lower-middle Eocene Allenby Formation, southern British Columbia (Crane and Stockey 1987) in 1991. The locality is 8 km north of Princeton, on the Princeton-Merritt Highway 5, approximately at the confluence of One Mile Creek and Summers Creek (universal transverse Mercator grid: UN 226940). Fossils are preserved as compressions in a finely laminated light green-gray shale that has been interpreted as a lacustrine deposit. Important components of the flora include *Betula leopoldae* (Crane and Stockey 1987), *Acer*, *Aesculus*, *Cercidiphyllum*, *Fagus*, *Prunus*, and rarer *Abies*, pine, and fern remains, although the flora is considerably more diverse than first apparent (Wehr, unpubl. data). Fossil and extant comparative material was photographed and scanned digitally for illustrations. Terminology follows that of the Leaf Architecture Working Group (1999).

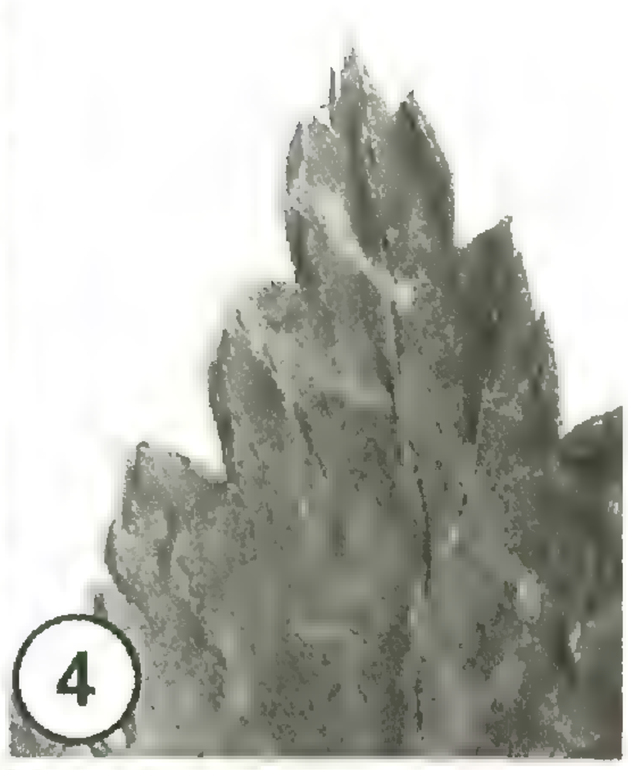
RESULTS

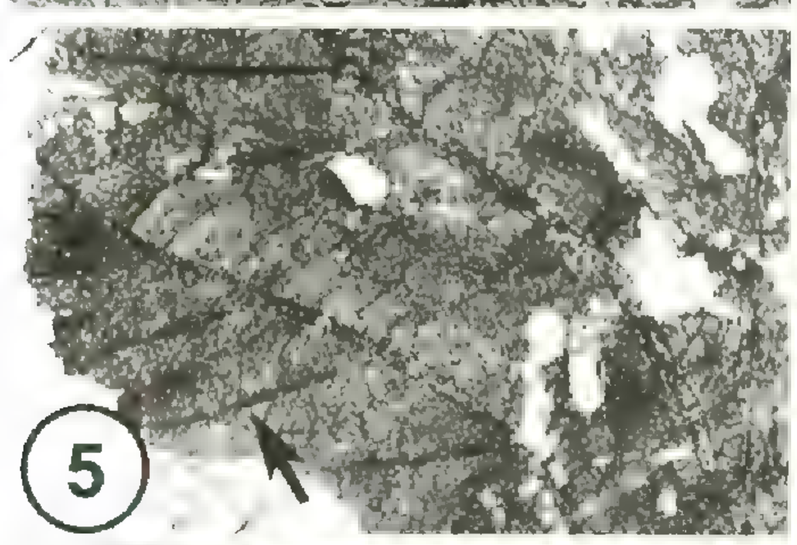
The description of *Neviusia dunthornei* is based on two specimens of leaf compressions. These specimens show details of leaf shape, margin, tooth morphology and several well-preserved orders of venation that can be compared favorably with extant *Neviusia* leaves, particularly those of *N. cliftonii* (Figures 1–20). In one specimen the leaf lamina is slightly folded basally but otherwise complete (Figures 1, 3, 7, 10). The second specimen is more fragmentary but bears excellently preserved detail of venation and leaf margin, and a partially preserved petiole (Figures 5, 12, 14–16). Leaves are up to 4.9 cm long and 5.6 cm wide (length/width ratio 0.88:1), elliptical to broadly ovate, and have up to seven palmately arranged lobes (Figure 1). The leaf apex is slightly acute at an angle of 88°, curves slightly, and is 1.4 cm long (Figures 1, 3), while the lateral lobes are up to 0.7 cm long. One specimen has a petiole that is preserved for 0.8 cm of its length that is up to 2.5 mm wide. While the leaf bases of both specimens are incompletely preserved they are estimated to have an obtuse angle of around 130°. The midrib is thick, up to 1 mm wide, and somewhat curved throughout its course, although this may be in part related to leaf preservation (Figures 1, 7). Secondary venation is craspedodromous with up to seven pairs of relatively broad, subopposite-ly attached, secondary veins extending from the midrib at an angle of around 30° in the lobes in upper 2/3 of the leaf (Figures 1, 3, 20).

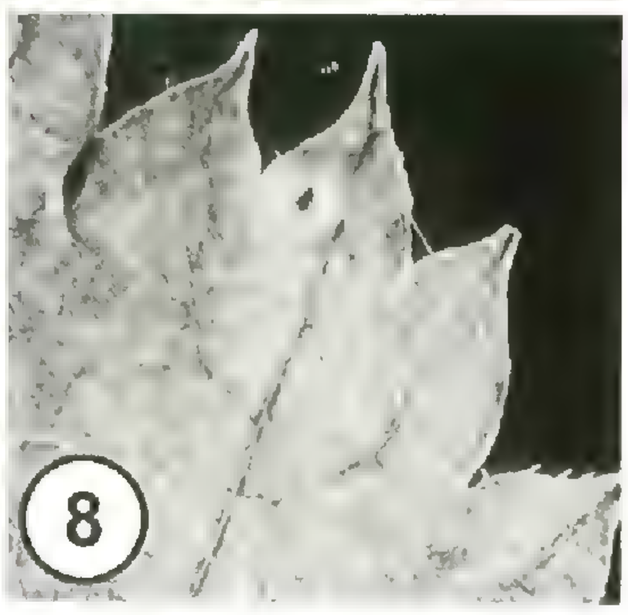


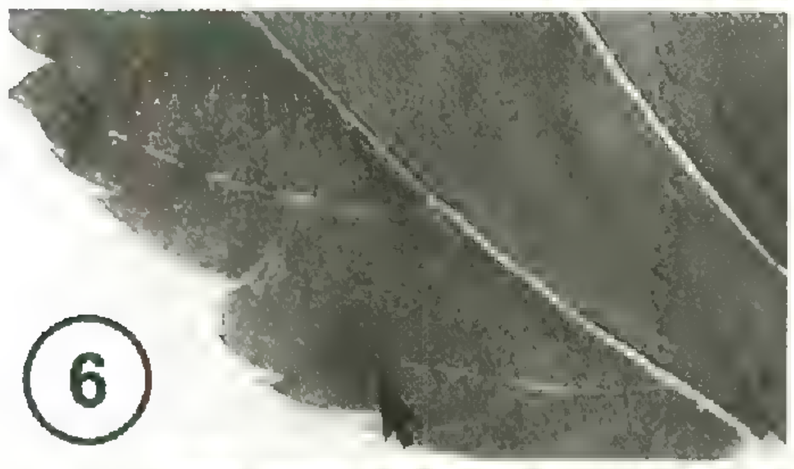
Figures 1–2. Fossil *Neviusia dunthornei sp. nov.* and extant *N. cliftonii* leaves, natural size. 1. *N. dunthornei*, holotype specimen (UWBM *54169*). 2. *N. cliftonii*.

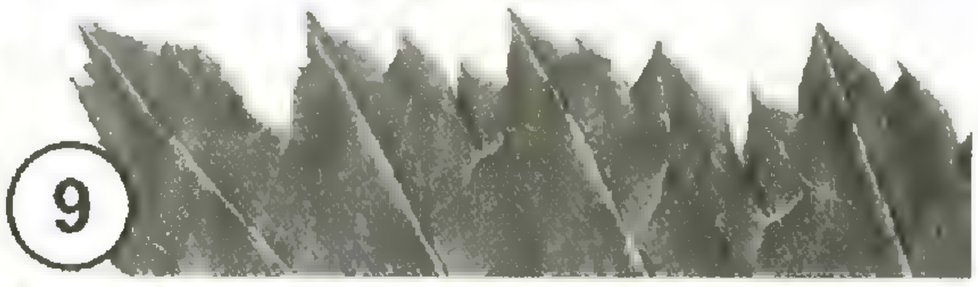


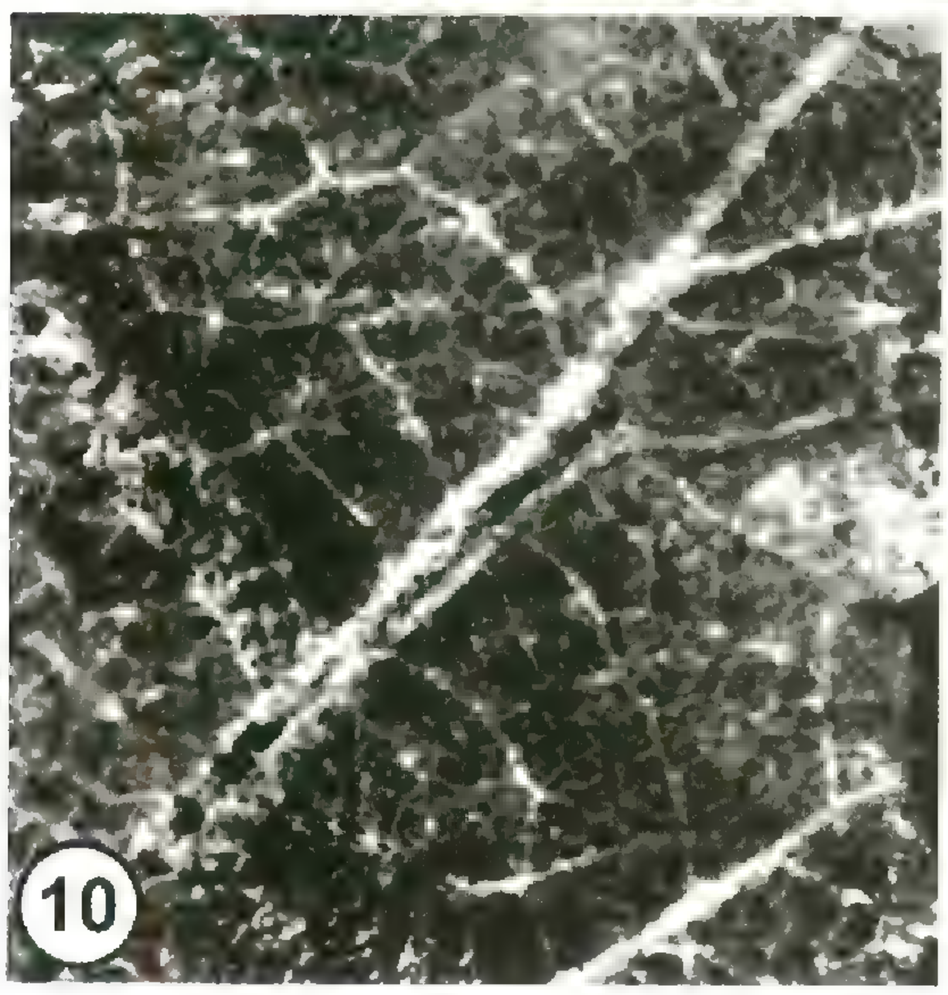




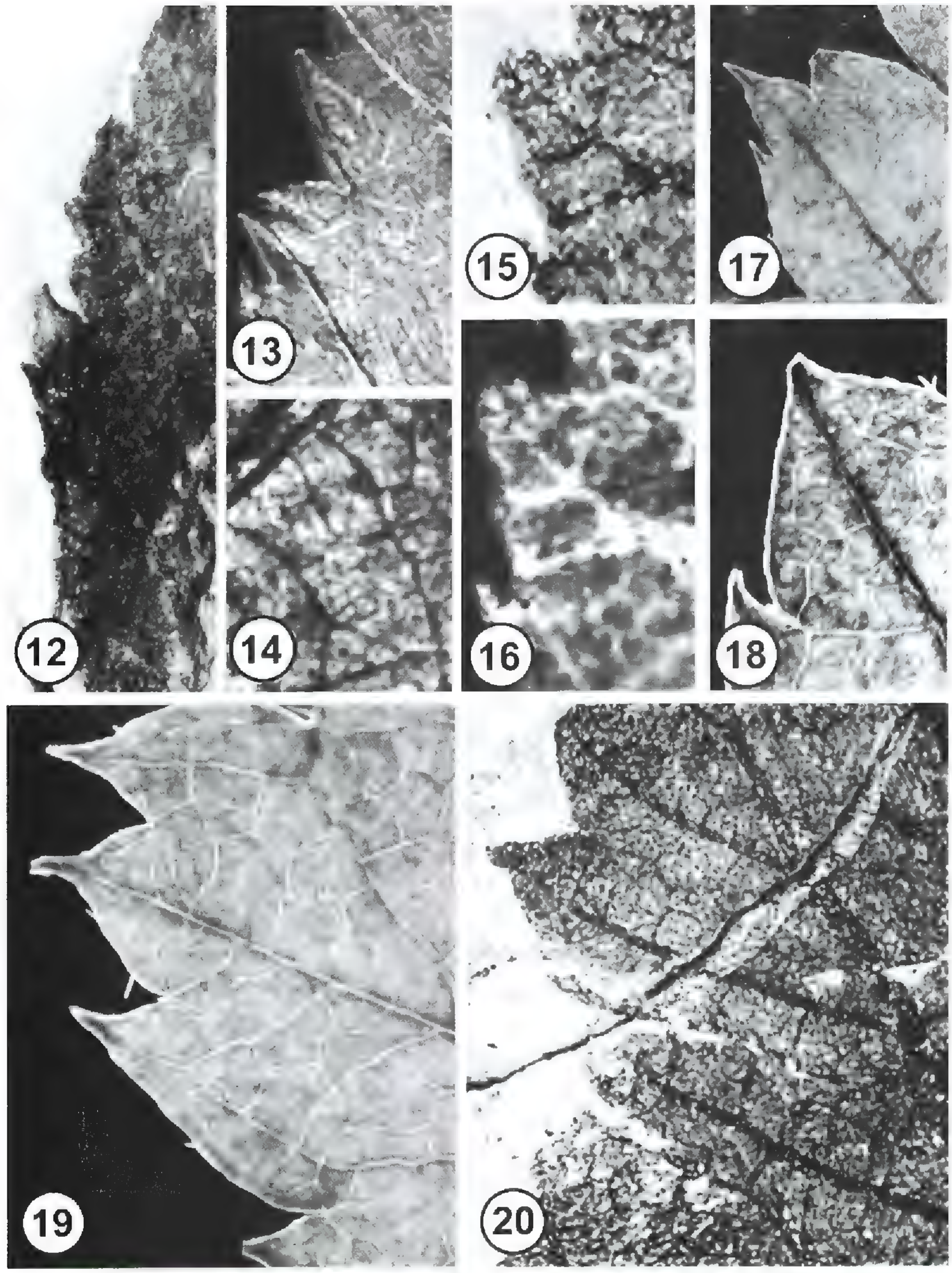








Figures 3–11. Details of leaf morphology and venation. Figures 3, 5, 7, and 10 are of the fossil leaf, *Neviusia dunthornei*; Figures 4, 6, 8, 9, and 11 are of the extant species, *N. cliftonii*. Figs. 3 & 4. Leaf apex, × 3.5. Figs. 5 & 6. Basal leaf area, showing compound agrophic veins (at arrow), × 2.1. Fig. 7. Midvein showing subopposite arrangement of secondaries, × 7. Fig. 8. Detail of teeth, × 6. Fig. 9. Overview of margin, × 2.2. Figs. 10 & 11. Detail showing secondary, tertiary, and higher order venation and aeroles, × 10.



Figures 12–20. Details of leaf margin and tooth morphology. Figures 12, 14–16, and 20 are of the fossil leaf, *Neviusia dunthornei*; Figures 13 and 17–19 are of the extant species, *N. cliftonii*. Fig. 12. Overview of margin, × 3.2. Fig. 13. Leaf margin, showing crowded teeth, × 10. Fig. 14. Detail of higher order venation, × 15. Figs. 15 & 16. Detail of tooth from fossil leaf to show venation, × 6; note accessory veins; Figure 15 is a negative image to increase contrast. Figs. 17 & 18. Detail of tooth venation, × 10; note accessory veins. Fig. 19. Margin showing teeth and details of venation, × 10. Fig. 20. Margin showing teeth and venation, × 6.

Compound agrophic veins, composed of four to six tertiaries each, extend from secondaries to the margin in the basal part of the leaf at angles of 25–30° to vascularize the marginal teeth at the tips of the lobes (Figures 1, 5, at arrow). Third-order veins form moderate, convex to sinuous curving braces between adjacent secondary veins that are perpendicular to the midrib, between secondary and agrophic veins and between adjacent agrophic veins (Figures 5, 10, 20). Fourth- and fifth-order veins are regular polygonal reticulate. Aeroles are well developed and 5+ sided (Figures 10, 14, 20).

The leaf margin is serrate with two to three sizes of regular and accessory teeth (Figures 3, 12, 15, 16, 20). Regular teeth occur at around 3 mm intervals, either singly or paired and grouped with one or two accessory teeth. Regular teeth are 2 mm long, flexulous apical, flexulous basal (Figures 3, 15, 16, 20). Each regular tooth is vascularized medially by an agrophic tertiary vein, with additional smaller accessory veins entering the vein on either side (Figures 3, 12, 15, 16, 20). Accessory veins are around 1 mm long and concave apical, flexulous basal to straight apical, flexulous basal (Figures 3, 12, 16).

DISCUSSION

Neviusia dunthornei is assignable to the genus *Neviusia* on the basis of distinctive features of the leaf shape, venation, and leaf margin. Whereas the tribe Kerrieae was established on the basis of floral features, the included taxa also have leaves with distinctive morphology. The Rosaceae encompasses a wide array of leaf morphologies, including clearly simple leaves that are entire to lobed as well as leaves that are so deeply dissected as to appear palmately and pinnately compound (Wolfe and Wehr 1988). Many rosaceous leaves have a serrate margin. However, a survey of leaf types within the family shows that entire and simply-lobed leaves typically have either a single, very regular type of tooth (e.g., many *Prunus* leaves) or, if more than one size order, the teeth are of the same type (e.g., *Malus*). Leaves of the tribe Kerrieae are unusual in having entire to lobed leaves with a serrate margin with 2 to 3 size orders of teeth of differing morphologies (regular teeth are flexulous apical, flexulous basal; accessory teeth may be concave apical, flexulous basal to straight apical, flexulous basal). Other rosaceous leaves with complex tooth marginal patterns of the type seen in Kerrieae otherwise usually occur in groups typified by highly dissected laminae, such as the blackberries (*Rubus*).

The three genera that compose the tribe Kerrieae can also be distinguished from one another based on several features of leaf morphology, venation, and margin. *Kerria* leaves are narrow and ovate with a length/width ratio of 2.1–2.5:1, and often have a long, attenuated leaf apex. *Rhodotypos* leaves are generally more isodiametric with a length/width ratio around 1.1:1 and have subopposite secondary veins, in contrast to the more distinctly alternate secondaries more characteristic of *Kerria* and *Neviusia*. Tertiary veins are considerably denser in *Kerria* and *Rhodotypos* than in *Neviusia*, and also tend to be more consistently perpendicular to the secondaries, while those of *Neviusia* are more variable and can sometimes result in an inverted V ("chevron") pattern.

Of the two extant species of *Neviusia*, the fossil is considerably more similar to *N. cliftonii* of the Mount Shasta region of northern California (Figures 2, 4, 6, 8, 9, 11). Both of these leaves are broadly ovate with secondaries that are subopposite from one another (Figures 5, 7, 8). The leaf margins in both are serrate with 2–3 orders of relatively coarse teeth with comparable shapes and venation patterns (Figures 10–20). In contrast, leaves of *N. alabamensis* are more elongate, have much finer teeth at the margin, and have secondary veins that are more pronouncedly alternate. Details of leaf margin are very similar in the fossil and *N. cliftonii*. They show similar variation in tooth size (Figures 3, 9), tooth morphology (Figures 3, 4, 8, 17–20), distribution of different morphological types (Figures 3, 6, 9, 12), and even degree of crowdedness (Figures 3, 12, 13, 18). The fossil differs from both extant species in having thicker midrib and primary veins (Figure 7).

Phytogeographic significance. The fossil record of the entire tribe Kerrieae is limited to this northwestern occurrence of *Neviusia* (Wehr and Hopkins 1994). Together with its modern distribution, the occurrence of *Neviusia* in the Okanogan Highlands suggests that the Kerrieae radiated from Asia into western, and subsequently southeastern North America, but never became a major North American element. It is interesting that *N. cliftonii*, the California native, has what might be considered less derived features (based on trends found in other tribes of Rosaceae) in comparison to the southeastern *N. alabamensis*. These include a loss of petals and an increase in number of stamens. This species also has a generally more elongate style as well as more lanceolate leaves than *N. cliftonii* (Shevock et al. 1992). The similarity of *N. cliftonii* and the fossil *N. dunthornei* leaves is consistent with an origin or early diversification of the genus in the Northwest, with

montane northern California serving as an early refugium, while forms that made it to the warm temperate Southeast apparently diversified further. It is notable that *Neviusia* has not been found in the extensive Eocene floras of the Mississippi Embayment, such as those of the Claiborne Formation (Dilcher 1971). The lack of Rosaceae in southeastern floras that are generally contemporaneous with Okanogan Highlands floras may be because of warmer regional conditions that at that time produced a more megathermal, possibly dry-adapted flora dominated by Lauraceae and early legumes (Graham 1999). Perhaps the arrival of *Neviusia* in southeastern North America occurred much later in conjunction with the climatic deterioration of the Neogene.

TAXONOMIC TREATMENT

Neviusia dunthornei DeVore, Moore, Pigg & Wehr, *sp. nov.*

Family: Rosaceae

Tribe: Kerrieae

Genus: *Neviusia* A. Gray.

TYPE SPECIES: *N. alabamensis* A. Gray

SPECIES DIAGNOSIS: Leaves broadly ovate, lobed; 4.9 cm long × 5.6 cm wide; L/W ratio 0.88:1; apex acute; midrib thick; venation craspedodromous; secondary veins forming acute angle, 30° to midrib, subopposite; compound agrophic veins forming acute angles 25–30° with secondaries; tertiaries forming moderate, curving braces between adjacent secondaries, secondaries and agrophic and adjacent agrophic veins; areoles 5–6 sided with freely ending veinlets; 4th and 5th order veins regular polygonate reticulate; margins serrate, two (occasionally three) size orders of regular and accessory teeth, regular teeth occurring at 3 mm intervals, solitary or paired, grouped with one or two accessory teeth, regular teeth 2 mm long, flexulous apical flexulous basal, vascularized medially, often with two lateral accessory veins, accessory teeth 1 mm long, concave apical flexulous basal to straight apical flexulous basal.

HOLOTYPE: UWBM *54169* (Figures 1, 3, 7). Collected by *Peter Dunthorne*, 1991.

PARATYPE: UWBM *97148* (Figures 5, 11, 19). Collected by *Peter Dunthorne*, 1991.

Type locality: CANADA. British Columbia: One Mile Creek, near Princeton (UWBM *B 3389*; *Crane & Stockey*, 1987).

Age and Stratigraphy: Allenby Formation, Lower-Middle Eocene.

ETYMOLOGY: The specific epithet, *dunthornei*, is named in honor of Peter Dunthorne of Sedro-Woolley, Washington, for his numerous contributions to the collecting of the Okanogan Highlands floras.

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INFERRING GENET DEVELOPMENT: INTERPLAY OF MERISTEM COMMITMENT AND GENET INTEGRITY

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ABSTRACT. Canada mayflower (*Maianthemum canadense*) is a rhizomatous, perennial herb whose genets consist of multiple ramets. In a given year, ramets exist as either flowering or vegetative shoots. The production of a flowering shoot requires the commitment of the apical meristem. The identity of ramets (vegetative, flowering, or absent) directly basipetal and acropetal to a focal ramet along a linear rhizome is here termed the context of the focal ramet. A given ramet may transition from one context to another over a given year. Transitions in shoot type (a consequence of meristem commitment) occur within a developmental phase while transitions involving loss of genet integrity (a consequence of fragmentation) result in a change in phase. Each ramet begins as an acropetal ramet and transitions through several phases before becoming "isolated" (not connected to a basipetal or acropetal ramet). In this study, ages of ramets varied significantly, with flowering shoots more likely to be produced by older ramets than vegetative shoots. Isolated ramets were older on average than ramets in all other phases. The contexts and phases occupied by vegetative ramets differed significantly from those occupied by flowering ramets. Ramets producing a flowering shoot were more likely than expected to be isolated ($> 50\%$ in both years) while isolated ramets with a vegetative shoot were more likely than expected to produce a flowering shoot in the following year. Ramets with a vegetative shoot were more likely than expected to produce a vegetative shoot next year if the ramet was connected to both basipetal and acropetal ramets.

Key Words: ramet, genet, meristem, Canada mayflower, Liliaceae, *Maianthemum*

Clonal plant populations may exist as an assemblage of genets, where a genet is all the plant material derived from a single zygote (Eriksson and Jerling 1990). Each of these genets, or genetic individuals, may in turn exist as a population of potentially independent ramets (Cook 1985), where ramets are the fundamental units of plant architecture that are iterated during clonal growth (Harper 1977). How these ramets, collectively derived from a single seed, exist within the genet may vary along a continuum of organization (Harper 1985). At one end of this

continuum is a genet that consists of all connected ramets and at the other end is a genet composed of all isolated ramets. In between these extremes, a genet may exist as a group of genet fragments, each composed of a variable number of connected ramets (Tuomi and Vuorisalo 1989).

The potential for "connectedness," or integration, of a species is thought to be of ecological and evolutionary significance and is the consequence of the interplay of forces promoting fragmentation and connectedness of genets. Evolutionary factors promoting fragmentation include the potential for disease spread through connections, the respiratory cost of connections, and localization of damage through disturbance. Those factors promoting connectedness include buffering of spatial variation, increased survivorship of ramets/genets through translocation of resources, and control of spatial spread to reduce intra-clonal competition (Abrahamson 1980; Cook 1985; Hutchings and Bradbury 1986; Hutchings and Mogie 1990; Pitelka and Ashmun 1985).

Canada mayflower (*Maianthemum canadense* Desf.) is a rhizomatous, perennial herb common to the understory of forests in New England. Canada mayflower is clonal with genets consisting of multiple ramets. Ramets consist of a rhizome with several nodes and an erect shoot. Each node is composed of 2–3 scale leaves, an axillary bud, and several adventitious roots (Kana 1982). Rhizome growth is sympodial with a ramet added to the genet through the activation of a lateral bud at the base of an erect shoot or an axillary bud at a node (Kana 1982).

Erect shoots are separated by an average of 12.5 cm (Ganger 1998) and their growth is essentially monopodial. A new vegetative shoot (an aerial leaf with 2–3 scale leaves and an axillary bud) is produced each year on the same axis. The growth of this axis ceases with the production of a flowering shoot (a stem, 2–3 leaves, and a terminal inflorescence). Regrowth of the erect shoot occurs with the activation of one of the previously produced subtending axillary buds (Kana 1982; Figure 1).

In the fall, vegetative shoots abscise leaving behind an overwintering bud that is preformed to become either a vegetative shoot (if an axillary bud) or a flowering shoot (if an apical bud) in the following year. Allocation of the appropriate meristem (apical or axillary) occurs at least as early as May in the year preceding emergence (Kana 1982). Whether the bud represents a vegetative or flowering shoot is here termed "bud type."

It is possible to age ramets and determine their reproductive history (whether the shoots of a given ramet have been vegetative or flowering in each year), since the vegetative and flowering shoots result from the

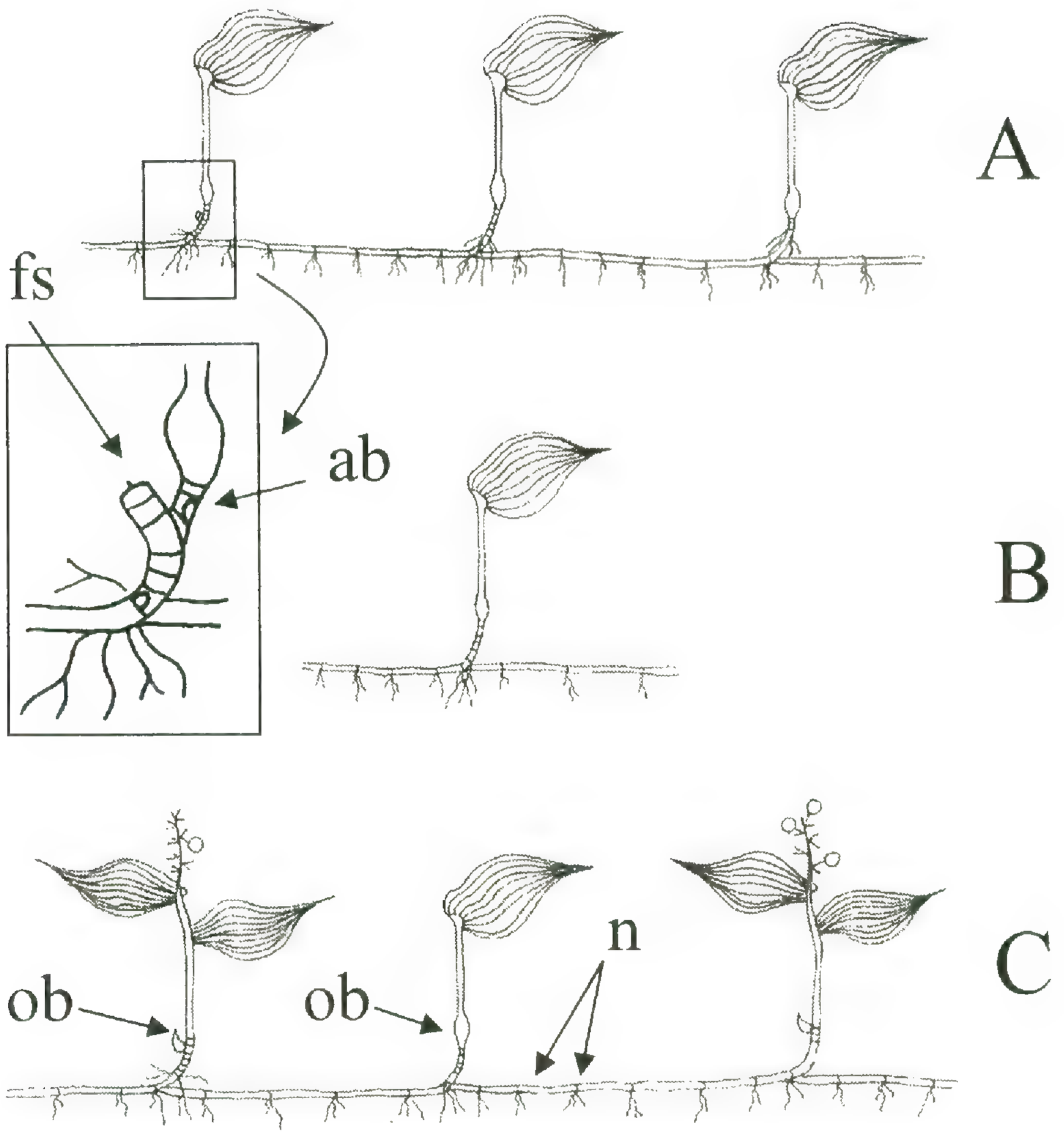

Figure 1. Three contexts of *Maianthemum canadense* are presented: A. A vegetative ramet with a vegetative ramet both basipetal and acropetal. B. A vegetative ramet with no ramet basipetal or acropetal. C. A vegetative ramet with a flowering ramet both basipetal and acropetal. n = node, fs = flowering shoot scar, ab = axillary bud, ob = overwintering bud. Note the different appearance of these buds on flowering and vegetative ramets.

commitment of different meristems and the scarring from abscission in the fall is distinctive for vegetative and flowering shoots (for a detailed explanation see Ganger 1997, Kana 1982). Hereafter, a "vegetative ramet" is defined as a ramet whose erect shoot is in the vegetative condition in the current year, and a "flowering ramet" is defined as a ramet whose erect shoot is in the flowering condition in the current year.

The habit of Canada mayflower and similar clonal plants presents an interesting situation where commitment of an apical meristem is possible and this "decision" is also being made by adjacent ramets on the same rhizome system. Adjacent ramets include the basipetal ramet, toward older tissue, and the acropetal ramet, toward younger tissue (Figure 1). Ramets are probably experiencing different physiological and microenvironmental conditions (Marshall 1990) and these differences may or may not lead to commitment of their apical meristem. If the commitment of a ramet's apical meristem is influenced by other ramets of the same genet then adjacent ramets are likely to have a greater effect than more distant ones (Cook 1985; Vuorisalo et al. 1997). The influence of adjacent ramets may vary as their identity varies (whether they currently exist as flowering shoots, vegetative shoots, or are absent). In the extreme case, a vegetative ramet connected to two vegetative ramets is potentially experiencing a different physiological condition than a vegetative ramet that is not connected to other ramets or is connected to two flowering ramets (Figure 1). The vegetative ramet in two of the three cases (Figure 1A and 1C) exists as part of a genet segment that includes three total ramets. In addition, these two focal vegetative ramets may have the same reproductive history and the same age. They do, however, differ from each other in the manner in which adjacent ramets on the same genet segment have committed meristems. Differences in states between these adjacent ramets may have an effect on how the vegetative ramets themselves commit meristems since adjacent ramets are part of the unique environmental background that ramets experience (Watson 1990). The identity (whether a vegetative shoot, flowering shoot, or not present) of these adjacent ramets (basipetal and acropetal) is here termed the "ramet context" of a focal ramet.

Fifteen distinct contexts are possible for Canada mayflower. These contexts are possible for both vegetative (15) and flowering (15) ramets, therefore, there are 30 total combinations (Figure 2). Moreover, ramets are likely to transition from one context to another over a given year. These include 1) transitions due to the commitment (or lack of commitment) of an apical meristem and 2) transitions due to fragmentation, which is the loss of connection between two ramets. These transitions may be due to mortality of the basipetal, acropetal, or both ramets or may be due to decay of the rhizome between ramets (Figure 1A). Contexts may then be grouped into six "phases:" A) a flowering or vegetative ramet basipetal and no ramet yet produced acropetally, B) no ramet basipetal (either dead or decayed rhizome) and no ramet yet produced acropetally, C) no ramet basipetal and either a vegetative or flowering ramet acropetal, D) either

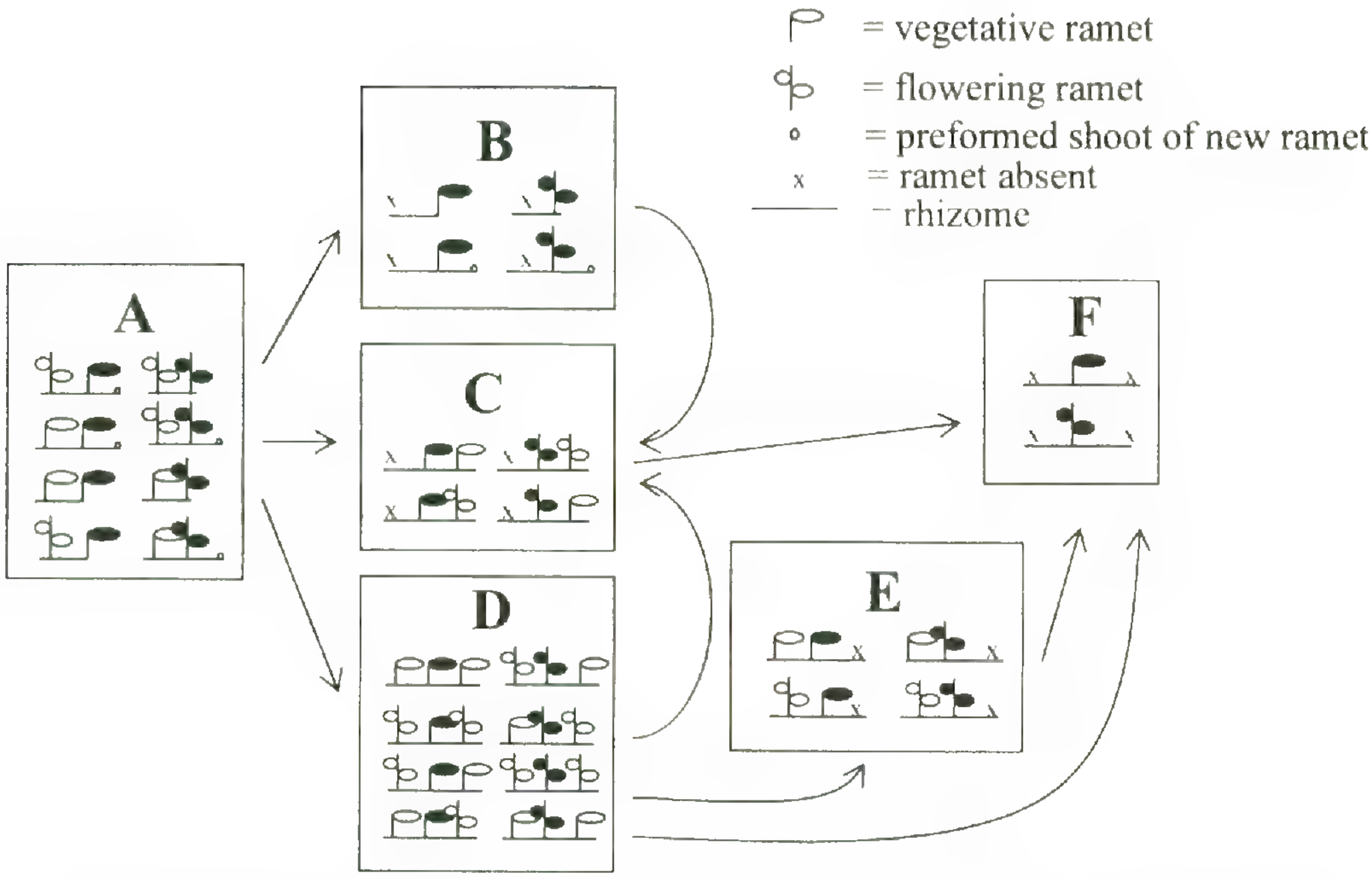

Figure 2. Six phases of *Maianthemum canadense* are presented (A–F). Each phase consists of multiple contexts. Black leaves indicate the focal ramet. Arrows indicate possible transitions from one year to the next.

a vegetative or flowering ramet both basipetal and acropetal, E) either a vegetative or flowering ramet basipetal and no ramet acropetal, and F) no ramet basipetal or acropetal (Figure 2). Transitions from one context to another within a phase are due to meristem commitments whereas changes in genet integrity necessitate transition from one phase to another.

The importance of context and phase in understanding how genets develop and how meristems are committed is not known. A two-year experiment was undertaken with Canada mayflower in order to answer the following questions: 1) What are typical ramet contexts? 2) Does ramet age vary with phase? 3) Is the distribution of vegetative and flowering ramets independent of phase? 4) Is the commitment of the apical meristem independent of phase? and 5) Is the commitment of the apical meristem related to estimated leaf surface area of vegetative ramets?

MATERIALS AND METHODS

In early spring of 1997, seven sites were identified, based on the presence of Canada mayflower, within the University of New Hampshire College Woodlands, Durham, NH (43°5.5′ north latitude, 71°25′

longitude). Sites were separated by at least 50 m. Within each site, two plots were delineated that were separated by < 1 m. Prior to emergence of shoots in one of the plots, 30 buds were identified that would become flowering shoots. In the other plot, 20 buds were identified that would become vegetative shoots. Flowering and vegetative shoots were identified in separate plots in order to increase the likelihood that vegetative ramets were physically independent of flowering ramets and meet the assumption of independence for the statistical analyses.

At the end of the fruiting season, genet segments were excavated to include the focal ramet (vegetative or flowering) and any ramets basipetal and acropetal on the same rhizome. Genet segments were labeled and taken to the laboratory. A similar procedure was followed in 1998 involving seven separate sites (consisting of two patches each) that were distinct from those in 1997.

Typical ramet contexts were divided into two subcategories: flowering ramet contexts and vegetative ramet contexts. The reason for this division was that in local populations, the frequency of flowering ramets can vary dramatically among sites (Silva et al. 1982; Worthen and Stiles 1986; Ganger, unpubl. data) and ramet contexts may differ between vegetative and flowering ramets. In this way the determination of typical ramet contexts will not be biased by the frequency of flowering ramets in a site.

For each genet segment excavated, the ramet context was determined and classified based on the identity of the ramet basipetal and acropetal on the same rhizome system: 1) no ramet basipetal or acropetal (0,0), where no ramet indicates that there is either a dead ramet or that the rhizome has decayed such that any physical connection that may have existed is no longer present; 2) vegetative ramet basipetal and no ramet acropetal (v,0); 3) no ramet basipetal and a vegetative ramet acropetal (0,v); 4) a vegetative ramet both basipetal and acropetal (v,v); 5) a flowering ramet either basipetal or acropetal (f); and 6) the presence of a newly activated lateral bud at the base of the ramet that results in a new rhizome and a new ramet acropetal, regardless of basipetal condition (b).

In order to determine whether flowering and vegetative ramets were equally distributed among contexts and phases (Figure 2), two separate three-way analyses were performed using a log-linear model (Sokal and Rohlf 1995; Wilkinson 2002). The log-linear models here are used to determine if observed frequencies of vegetative and flowering ramets in each context and phase for both years differed from expected frequencies. The expectation is that both vegetative and flowering ramets will be equally represented in each context and phase for both years.

An analysis of variance (ANOVA) was used to determine if age varied with phase. The dependent variable was ramet age. Variables included in the analysis were year, site {year}, phase, ramet type, and the two-way interactions. Year, phase, and ramet type were fixed factors, while sites were nested within year. The three-way interaction was not included due to a problem with the distribution of phases among ramets between years.

In order to determine if the commitment of the apical meristem by vegetative ramets was independent of phase, a three-way analysis was performed using a log-linear model (Sokal and Rohlf 1995; Wilkinson 2002). This analysis is used to determine if meristem commitment was independent of phase and year. This log-linear analysis included only vegetative ramets since regrowth of the shoot from a subtending axillary bud occurs after flowering. This bud is vegetative.

A regression analysis was performed to determine if estimated leaf surface area was related to the tendency for vegetative ramets to allocate the apical meristem. For vegetative ramets, the leaf surface area was estimated based on an established relationship between the leaf surface area (mm^2) and two linear measures (mm) of the leaf. The length (L) from the tip of the leaf to the base of the leaf and the width (W) of the leaf at the midpoint of the length segment together predict leaf surface area (area = 27.78*L + 55.00*W − 1198.16; $p < 0.001$, adjusted $r^2 = 0.94$; Ganger 1998).

RESULTS

Thirty-nine of 210 flowering ramets and 9 of 140 vegetative ramets from 1997 were lost or could not be accurately aged due to decay, and were excluded from the age analysis. Forty-two of 210 flowering ramets and 6 of 140 vegetative ramets from 1998 were excluded for similar reasons.

Flowering ramets and vegetative ramets were represented in each of the six contexts in both 1997 and 1998 (Table 1) and the distribution of these ramets was not independent of context (Pearson $\chi^2_{16,\ 0.05} = 98.6$, $p < 0.001$). Deviations of the multiplicative parameter estimates from one (Wilkinson 2002) were used to assess whether the frequency of ramets in each context differed from expected. The value that is compared to one is given in parenthesis for each comparison. A value close to one indicates frequencies approaching expected while values far from one indicate values much higher or lower than expected. Vegetative ramets were more likely than expected to be connected to a vegetative ramet both basipetal and acropetal (1.52) than were

Table 1. The distribution of vegetative and flowering ramets in each of the *Maianthemum canadense* ramet contexts for both 1997 and 1998. 0 = no ramet or dead ramet, v = vegetative ramet, f = flowering ramet, and b = growing rhizome or new acropetal bud. The first symbol in the pairs represents the basipetal ramet and the second, the acropetal ramet.

	1997				1998			
Ramet	v		f		v		f	
Context	n	(%)	n	(%)	n	(%)	n	(%)
0,0	35	(26.3)	102	(53.1)	59	(43.3)	114	(62.3)
0,v	37	(27.8)	46	(24.0)	40	(29.4)	34	(18.6)
v,0	10	(7.5)	11	(5.7)	5	(3.7)	3	(1.8)
v,v	23	(17.3)	10	(5.2)	9	(6.6)	6	(3.6)
f	6	(4.6)	18	(9.4)	0	(0.0)	16	(6.6)
b	22	(17.0)	5	(2.6)	23	(16.9)	10	(8.7)

flowering ramets. Vegetative ramets were also more likely than expected to have produced an acropetal ramet (1.83). Flowering ramets were more likely than expected to be connected to other flowering ramets (2.24) and to have no ramet either basipetal or acropetal (1.44). In fact, the majority of flowering ramets in both years existed with no ramet basipetal or acropetal (51.2% in 1997, 61.7% in 1998). There were more ramets in 1998 than expected within the no ramet basipetal or acropetal context (1.33). There were more ramets in 1997 than expected within the vegetative ramet basipetal and no ramet acropetal context (1.40).

The age of ramets varied with phase ($p < 001$; Table 2; Figure 3). Ramets in phase F were significantly older than ramets in all other phases (Bonferroni adjusted $p < 0.001$; Figure 3). Ramets in phase C were significantly older than ramets in phase A (Bonferroni adjusted $p < 0.05$; Figure 3). Flowering ramets were significantly older (mean = 5.4 years, SD = 1.98, SE = 0.11) than vegetative ramets (mean = 3.9 years, SD = 1.92, SE = 0.12; $p < 0.001$; Table 2; Figure 4).

Vegetative ramets were represented in each of the six phases in both years while flowering ramets were present in all except phase A in 1998 (Table 3). The distribution of vegetative and flowering ramets was not independent of phase (Pearson $\chi^2_{16,\ 0.05} = 87.6$, $p < 0.0001$). Deviations of the multiplicative parameter estimates from one indicated that more vegetative ramets than expected occurred in phases A (3.0) and B (1.3). Similarly, more flowering ramets than expected occurred in phases B (1.3), E (1.5), and F (1.8).

Twenty-five percent of vegetative ramets produced a flowering bud in 1997, while 18% produced a flowering bud in 1998. The distribution of

Table 2. Results of analysis of variance using age as the dependent variable. Y = year, P = phase, R = ramet shoot type. Adjusted $r^2 = 0.29$.

Source	df	MS	F	*p*-value
Year	1	14.53	1.20	NS
Site {year}	12	12.16	3.70	<0.001
Phase	5	37.09	11.30	<0.001
Ramet shoot type	1	60.96	18.57	<0.001
Y*P	5	0.67	0.20	NS
Y*R	1	0.06	0.02	NS
P*R	5	2.67	0.81	NS
Y*P*R				
Error	582	3.28		

vegetative and flowering buds was not independent of phase (Pearson $\chi^2_{16,\ 0.05} = 32.0$, $p < 0.01$). Deviations of the multiplicative parameter estimates from one indicated that more vegetative buds than expected occurred in phases A (1.7) and D (1.4). Similarly, more flowering buds than expected occurred in phases B (1.3) and F (1.5).

The estimated leaf surface area of vegetative ramets ranged between 1122 mm^2 and 4880 mm^2 in 1997, and 737 mm^2 and 3635 mm^2 in 1998. Vegetative ramets that produced a flowering bud had significantly larger leaf surface area than ramets that produced a vegetative bud ($F_{1,\ 254,\ 0.05} = 22.51$, $p < 0.001$). No vegetative ramet in either year with a leaf surface area of less than 1371 mm^2 produced a flowering bud.

DISCUSSION

Clonal plants exist as a hierarchy of organization that includes meristems, ramets, genet fragments, and genets. Here an attempt is made to place ramets, the functional units of plant construction, within the context of genet fragments to determine whether the genet fragment level of organization offers additional insights into meristem determinations made by ramets that the ramets alone would not provide.

A ramet existing as a vegetative shoot in year x may be either a vegetative shoot or a flowering shoot in year x+1. Ramets that exist as a flowering shoot in year x appear to be programmed to be a vegetative shoot in year x+1. Ramets have the potential, then, to transition between vegetative and flowering shoots. A ramet appears to flower at a maximum rate of once every two years. The rate at which mayflower ramets flower is much lower than the theoretical maximum.

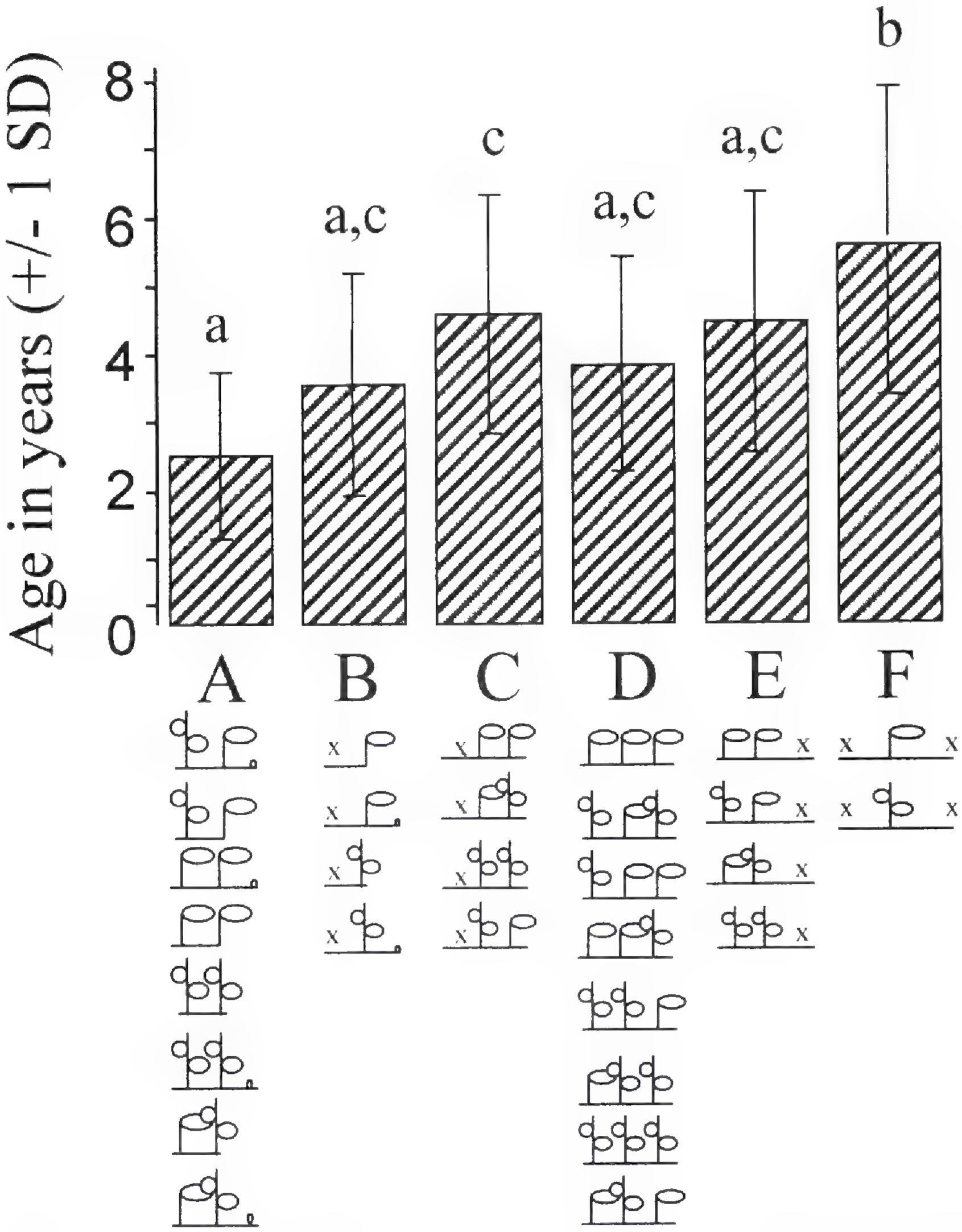

Figure 3. Ages of *Maianthemum canadense* ramets in the six phases. Small case a–c indicate means that are not significantly different. SD = standard deviation.

Despite the fact that ramets may transition between vegetative and flowering shoots, there is a significant difference in the contexts of ramets existing as vegetative and flowering shoots. It is possible that differences in their contexts represent a pre-flowering and post-flowering existence. This difference in the distribution of vegetative and flowering ramets among contexts is most evident in that vegetative ramets were more likely to be connected to one or both adjacent ramets (73.7% of ramets in populations in 1997 and 56.7% of ramets in populations in 1998; Table 1). Flowering ramets were more likely to be separated from

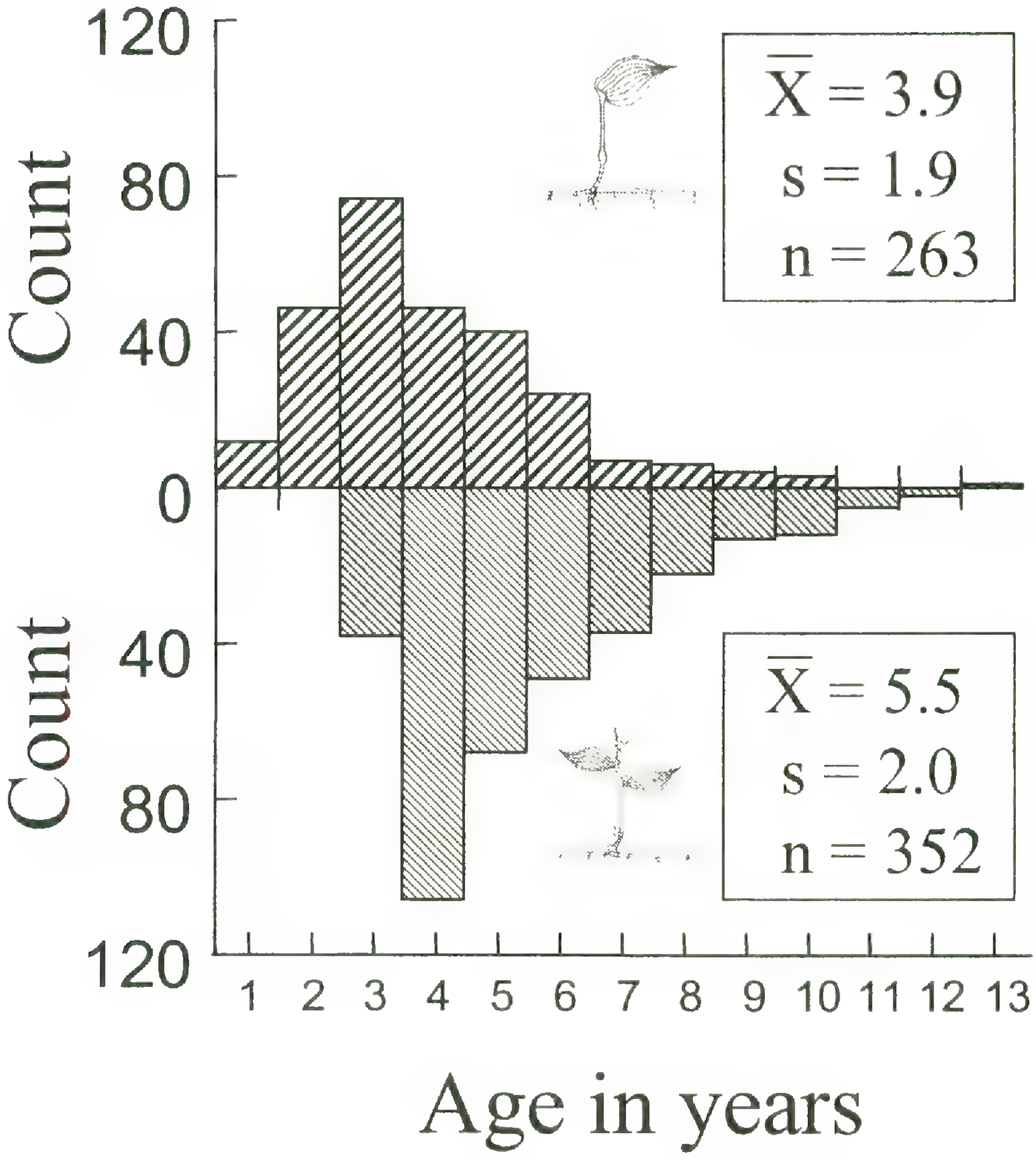

Figure 4. Distribution of the ages of *Maianthemum canadense* ramets. Vegetative ramets and flowering ramets are presented separately.

adjacent ramets, in populations of ramets in both 1997 (53.1%) and 1998 (62.3%; Table 1). The average age of flowering ramets coincided with the average age of isolated ramets in general, indicating that at least statistically, ramets are likely to flower at about the same time that they become isolated. The potential for adjacent ramets in many clonal plant species to provide photosynthates to ramets experiencing stress or periods of high resource demand, for example flowering and fruiting, is well documented (Hartnett and Bazzaz 1983; Jónsdóttir and Callaghan 1989; Turkington and Harper 1979; Yu et al. 2002). Isolated ramets would not be able to reap the benefits of integration in the year of flowering. This appears to set up an important distinction between isolated and connected flowering ramets. Do these two populations of

Table 3. The distribution of *Maianthemum canadense* ramets among phases for both 1997 and 1998. v = vegetative ramet, f = flowering ramet. Phases are illustrated in Figure 2.

	1997		1998	
Phase	v	f	v	f
A	9	1	4	0
B	13	4	19	10
C	39	56	40	42
D	27	14	9	10
E	10	16	5	8
F	35	102	59	114

flowering ramets (isolated versus connected) differ in their abilities to set and mature fruit? Or, conversely, have flowering ramets already accumulated sufficient resources independently or through prior photosynthate translocation during previous years when connections to adjacent ramets still existed?

Previous research with Canada mayflower suggests that under "typical" levels of fruiting, ramets are able to mature consistent numbers of seeds whether they are connected or experimentally isolated. Under augmented pollination, ramets were able to mature additional seeds if they were connected, but produced fewer seeds when they were experimentally isolated (Ganger 1997). Populations of flowering ramets were able to mature similar numbers of seeds whether they were flowering for the first or second time, and the relationship between the number of seeds and the average weight of these seeds was consistent between these two flowering ramet groups (Ganger 2000). The ability of a vegetative ramet to become a flowering ramet in the following year could then be thought of as an allocation response, one that is made once sufficient resources have been accumulated.

Phase also appears to be a useful construct, not just in helping to simplify the many transitions possible from context to context over a given year, but also in relating both age and the likelihood of allocating an apical meristem to changes in genet integrity. A ramet begins as a vegetative shoot, produced by a basipetal ramet. Many pathways through phases are possible from this point (Figure 2), but all pathways end ultimately in the same phase, that of an isolated ramet. Despite the existence of these multiple pathways, ramets occur with greater probability in certain phases. This pattern indicates that certain pathways are used more often as ramets mature. The average ages of ramets within phases may also be used to infer details about how the genet is developing

over time. The length of time it takes for the average ramet to produce an acropetal ramet is somewhat longer than 3.5 years. This conclusion is inferred from the average ages of ramets in phase A (2.5 years) and phase B (3.5 years). A ramet's loss of connection to its genet is likely to progress over 5.5 years since ramets in phase F are 5.5 years old on average. Movement into phase F represents the loss of connection to both the basipetal and acropetal ramet. In most cases it appears that the basipetal connection is lost before the acropetal connection since only 5.7% of vegetative ramets and 6.8% of flowering ramets existed in phase E. Conversely, 32% and 30% of vegetative ramets existed in phases B and C, respectively, and 4% and 28% of flowering ramets existed in phases B and C, respectively. A ramet is unlikely to remain connected to both a basipetal and acropetal ramet (phase D) for long, since few ramets were found in this phase (13.8% of vegetative ramets and 6.8% of flowering ramets) and the average age of ramets in this phase was 3.8 years.

The phase of a vegetative ramet was also related to the probability of it committing its apical meristem to flowering in the following year. Isolated vegetative ramets were more likely to allocate apical meristems. Many plants preform organs in one year for expansion in the next (Geber et al. 1997). Whether a bud is flowering or vegetative may be related not only to current conditions but to past conditions as well (Geber et al. 1997). That ramets exist in locations with distinct edaphic and climatic conditions is generally accepted (Marshall 1990). These microenvironmental conditions may have an effect on whether a ramet's apical meristem is activated. Environmental effects on ramets may be integrated by the genet. Therefore adjacent ramets may play a role in allocation decisions of a focal ramet. Results from this study suggest two hypotheses for further testing. The first hypothesis is that as the genet begins to fragment—particularly the connection between a focal ramet and its acropetal ramet—there is a loss of apical dominance. With the loss of apical dominance comes the ability of the focal ramet to allocate its apical meristem. The second hypothesis is that ramets pass through predictable phases as they age and that the fragmentation of the genet is correlated with but not the cause of the transition from vegetative to flowering shoot. Ramets may be thought of as accumulating resources that will promote flowering. The length of time that it takes to accumulate these resources coincides with the length of time that ramets tend to remain connected to adjacent ramets.

The estimated leaf surface area of vegetative ramets was strongly correlated with the likelihood that the vegetative ramet contained a preformed flowering shoot. These results are consistent with those

found by Williams (1985) for Canada mayflower and Geber et al. (1997) for mayapple (*Podophyllum peltatum*). These variables are correlated and as such it cannot be said that a larger surface area causes the commitment of an apical meristem, particularly since the bud primordia of vegetative shoots are visible under the microscope as early as May in the year prior to emergence (Kana 1982). It is entirely possible that larger leaf surface area is part of the process leading to flowering in that the greater surface area may lead to greater accumulated photosynthates.

The connections between ramets of a genet of Canada mayflower were classified as long-lived (> 2 years) by Pitelka and Ashmun (1985) using data from Silva (1978). Eriksson and Jerling (1990) classify Canada mayflower as a species with *integrated genets* as opposed to one with *genet splitters*. This classification is based in part on data from Sobey and Barkhouse (1977) that list distances between ramets on the same genet as > 40 cm. Forty cm is considered a short enough distance for translocation to still be cost effective while longer distances may result in an increased rate of disintegration (Eriksson and Jerling 1990). The length of time that inter-ramet connections must remain intact for a species to be considered an integrated genet is somewhat arbitrary. Among mayflowers, there appears to be great variation among genets in the length of time that these connections persist. Ramets as young as 2 years were found to have no ramet basipetal (phase C) and ramets as young as 1 year were found to have no ramet basipetal or acropetal (phase F). Conversely, ramets as old as 8 years were found to still have a ramet both basipetal and acropetal (phase D) and ramets as old as 9 years were found to still have a ramet basipetal (phase B). This variability may be as important as the average length of time that these connections persist in Canada mayflower since it suggests either phenotypic plasticity in the persistence of connections or the potential for genetic variation with respect to the persistence of connections. Effectively then, the responses ascribed to genets by Eriksson and Jerling (1990) may be responses of ramets. The overall effect of these ramet responses would be evident at the level of the genet. To the degree that genets appeared to act differently, there would be uniformity of action by ramets within a genet. If there is a great deal of phenotypic plasticity in disintegration behavior, then how genets are categorized becomes less important. If there is uniformity of behavior by ramets (i.e., low levels of phenotypic plasticity) within a genet, the genets may effectively be categorized.

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AN INVENTORY OF THE VASCULAR FLORA OF MORNINGSIDE NATURE CENTER, ALACHUA COUNTY, FLORIDA

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ABSTRACT. A floristic inventory of Morningside Nature Center in Alachua County, Florida, was conducted from May 2001 to April 2003. From the 112.5-hectare park, 527 vascular plant species were collected (not including hybrids). These included 9 ferns, 5 conifers, and 513 angiosperms (representing 103 families and 310 genera). Of the 527 species, 456 were native to North America north of Mexico and 71 were non-native but naturalized. Five plant communities are recognized in the park: pine flatwoods, which cover 53.6% of the park; sandhills, which cover 21.5% of the park; ruderal areas, which cover 20.1% of the park; cypress swamps, which cover 4.4% of the park; and flatwoods depressions, which cover 0.4% of the park. The plant families best represented at Morningside include the Asteraceae with 71 species, Poaceae with 60 species, Fabaceae with 42 species, Cyperaceae with 32 species, Ericaceae with 15 species, Lamiaceae with 15 species, and Euphorbiaceae with 14 species. The largest genera at Morningside include *Quercus* (11 species and 2 named hybrids), *Desmodium* (9 spp.), *Cyperus* and *Hypericum* (8 spp. each), and *Asclepias* and *Rhynchospora* (7 spp. each). Twenty-two species are new records for Alachua County. Nine species growing at Morningside were found to be at or near the northern or southern limits of their range. Finally, six Florida endemics (or near endemics) were found in the park.

Key Words: Morningside Nature Center, Alachua County, floristics, plant communities, Florida

The floristic study was conducted at Morningside Nature Center (Figure 1). This 112.5-hectare park is located at 3540 East University Avenue in Section 2, Township 10 South, Range 20 East, and Section 35, Township 9 South, Range 20 East, at 29°40′ N and 82°16′ W, in Gainesville, Florida. The elevation of the nature center is 46.3 meters above sea level. Morningside is bordered by state-owned lands to the north, the North Florida Evaluation and Treatment Center to the east, University Avenue to the south, and the Loften Center (part of Alachua County public school system) to the west. The living history farm uses 10 acres of the park (Johnson 1998).

Figure 1. Map of trails at Morningside Nature Center.

The land that was to become Morningside Nature Center was first recorded as being owned by Neamiah Brush in the early to mid-1800s. The first recorded use of the land was for producing turpentine by tapping the numerous pines. In 1903, A. R. Scruggs of Alachua County bought all of the land currently forming Morningside Nature Center and used it for timber and turpentine operations. In 1964, the City of Gainesville bought the land from the federal government for $80,820 and reserved the land for outdoor activities and recreation. Morningside Nature Center was established in 1970, with much help from Marjorie Carr and the Junior Welfare League. Marjorie Carr was a nationally recognized environmentalist in northern Florida. When she learned of the surplus land the city had purchased, she urged the Junior Welfare League to adopt the project of turning this land into a nature park. After the park was established, the Junior Welfare League donated $15,000

and added the Nature Center. In 1973, a living history farm was added to the park. Soon after, a longleaf-pine cabin, two twin-crib barns, a one-room schoolhouse, farm animals, and a vegetable garden were added.

Climate and weather. While northern Florida is geographically rather homogenous, Alachua County's climate differs from that of other North Florida counties because of its unique latitudinal location, distance from the sea, and the variety of surface features. Alachua County has two major seasons, a warm rainy season and a cooler dry season. The warm rainy season lasts from the middle of May to the end of September. About 60 percent of the precipitation occurs in these warm months. Rainfall usually occurs as afternoon thunderstorms, which are generated by surface heating and fed by the convergence of breezes from the Gulf of Mexico and the Atlantic Ocean. The most variable rain for the county is produced by frontal passages during the winter months. An average of 38 frontal systems pass through North Florida during the winter season, 29 during spring, 19 during summer, and 41 during fall according to records kept for 1965 through 1967 (Dohrenwend 1978).

Most of the rainfall in Alachua County occurs in the four months of June, July, August, and September. The most precipitation occurs in August with an average of 208 mm. The average annual rainfall for Gainesville is 1370 mm. November is the month with the lowest amount of rainfall (44 mm). Precipitation is extremely variable from year to year and may deviate from the mean by as much as 40%. Snow is infrequent, but when it occurs, it is light and does not normally accumulate or persist (Dohrenwend 1978).

The average annual pan evaporation for Gainesville is 1674 mm, although true evaporative loss is less than that of pan evaporation. The average annual solar radiation is 156,150 langleys. The greatest amount of solar radiation occurs in May and the least in January. The greatest year-to-year variation occurs in June (Dohrenwend 1978).

The average range in monthly temperature is approximately 13°C and the average difference between daytime and nighttime temperatures is also 13°C. The highest maximum shade temperature recorded was 40°C and the lowest winter temperature was –9°C. The average number of freezes per year is four. The average frost season is 70 days. The average annual soil temperature at a 10 cm depth is 23°C. The warmest month is July and the coldest is February, at that depth (Dohrenwend 1978).

The average monthly minimum humidity is almost always above 40%. There are a few summer days where humidity remains above 70%.

Alachua County usually has light winds. Ninety-five percent of all winds are less than 12 knots, 78% less than 9 knots, 56% less than 6 knots, and there is no measurable wind 22% of the time. The average wind speed for three years of recording was 3 knots. Year round, the winds usually come from the north during the night. During the day, however, the wind can come from any direction (Dohrenwend 1978).

Geology. Florida consists of five natural topographic divisions: the Central Highlands, Tallahassee Hills, Marianna Lowlands, Western Highlands, and Coastal Lowlands. Alachua County lies within the Central Highlands. This area extends from the Georgia state line south to Glades County and lies between the Withlacoochee and St. Mary's Rivers. This region is physiographically diverse and includes swampy plains, thousands of lakes, and hills. The soils are mostly sandy, the sand being derived from Pleistocene marine terraces, the Miocene Hawthorne formation, and the Pliocene Citronelle formation. The altitude varies from less than 12 meters above sea level to the highest point in the peninsula, 99 meters on the summit of Iron Mountain near Lake Wales. The many lakes in this area indicate the occurrence of shallow, soluble limestone below the surface (Cooke 1945).

Morningside is underlain by Ocala limestone. This limestone ranges from pure white to yellow, and is commonly granular in texture, but in some places has become compacted rock due to the deposition of travertine or calcite in its interspaces. In some locations, it is extremely porous because it consists of a loose mass of foraminifers, bryozoans, and other small organisms. The chemical composition of this limestone is extremely uniform. It mostly consists of carbonate of lime and contains as little as two-fifths of one percent of impurities. The thickness of this limestone layer has not been determined due to the erosion of the surface and the inability to identify the bottom (Cooke 1945).

Morningside is situated in the plateau-like region of Alachua County, which has a nearly level topography and ranges in elevation from 45 to 61 meters above sea level (Pirkle 1956). Loose sands at the surface in this area are underlain by an impermeable clay layer, resulting in a radial pattern of drainage from the plateau to surrounding areas.

Soils. There are fourteen different soil types at Morningside Nature Center. These soil types are closely correlated with the various plant communities occurring at Morningside. Candler fine sand, (soil type 2B) is a soil that is excessively drained and is found in deep, sandy uplands, supporting a sandhill community. Millhopper sand (soil type 8B) is

a moderately drained soil that is in irregularly shaped areas in sandhill uplands and slightly rolling hills in pine flatwoods. Tavares sand (soil type 20B) is a deep and sandy soil that is moderately well drained and supports pine flatwoods or sandhill communities. Chipley sand (soil type 28) is a poorly drained soil found in the flatwoods and in transition zones between the flatwoods and sandhills. Sparr fine sand (soil type 50) is a poorly drained soil that is found on rises in pine flatwoods and on smooth or slightly convex slopes in sandhills. Pelham sand (soil type 13), Pomona sand (soil type 14), Wauchula sand (soil type 17), Myakka sand (soil type 48), and Plummer fine sand (soil type 51) are all poorly drained soils supporting a pine flatwoods. Surrency sand (soil type 16) and Monteocha loamy sand (soil type 19) are very poorly drained and found in ponds and in wet depressions in pine flatwoods. Pomona sand, depressional (soil type 25), and Placid sand (soil type 34) are very poorly drained soils in pine flatwoods depressions and drainageways, usually dominated by species characteristic of cypress swamps (Soil Conservation Service 1985).

MATERIALS AND METHODS

A floristic inventory of Morningside Nature Center was conducted from May 2001 to November 2002. Plants were collected by walking through all parts of the park. A map of trails (Figure 1) was used to determine which areas of the park had been thoroughly sampled. Each area of the park was visited as often as possible to ensure proper sampling. The shallow stream on the east side of the park was sampled by walking in it as far as it extended on the Morningside property.

At least two voucher specimens of each species were collected, one being deposited in the University of Florida Herbarium (FLAS) and the other in the Morningside herbarium. Both FLAS and the Morningside herbaria were searched for additional species collections from the park. The plant specimens were identified using mainly Wunderlin (1998), and often referencing Campbell (1983), Clewell (1985), Hall (1978), Wunderlin (1982), and Wunderlin and Hansen (2003).

RESULTS

A total of 536 taxa, including 527 species, were found in 310 genera, which were included in 103 families. These are listed in the Appendix. The largest families, followed by number of species, are Asteraceae (71 spp.),

Poaceae (60), Fabaceae (42), Cyperaceae (32), Ericaceae (15), Lamiaceae (15), Euphorbiaceae (14), Apiaceae (12), Fagaceae (11 plus 2 named hybrids), Plantaginaceae (11), and Rubiaceae (10). The largest genera are *Quercus* (11 spp. plus 2 named hybrids), *Desmodium* (9), *Cyperus* (8), *Hypericum* (8), *Asclepias* (7), *Rhynchospora* (7), *Andropogon* (6), *Dichanthelium* (6), *Ludwigia* (6), *Polygala* (6), *Smilax* (6), and *Xyris* (6).

Twenty-two species are new records for Alachua County. These include *Agalinis purpurea*, *Aristida gyrans*, *Bulbostylis stenophylla*, *Cirsium nuttallii*, *Commelina benghalensis*, *Dalea carnea* var. *carnea*, *Desmodium viridiflorum*, *Dichanthelium strigosum* var. *leucoblepharis*, *Hypericum brachyphyllum*, *Juniperus virginiana*, *Liatris tenuifolia* var. *tenuifolia*, *Ludwigia erecta*, *L. virgata*, *Lygodium japonicum*, *Pogonia divaricata*, *Populus deltoides*, *Sabatia brevifolia*, *Sorghastrum secundum*, *Symphyotrichum adnatum*, *Trichostema setaceum*, *Utricularia juncea*, and *Yucca aloifolia*. Six Florida endemics were also found. These are *Asimina reticulata*, *Arnoglossum floridanum*, *Berlandiera subacaulis*, *Callisia ornata*, *Chrysopsis subulata*, and *Verbesina heterophylla*.

Three species found at Morningside are listed as threatened by Coile (2000): *Pogonia divaricata*, *Sarracenia minor*, and *Zephyranthes treatiae*. *Ctenium floridanum* is listed as endangered (Coile 2000; Florida Natural Areas Inventory 2002). *Osmunda cinnamomea*, *O. regalis*, and *Rapidophyllum hystrix* are listed as commercially exploited (Coile 2000). Ward (1979) listed two of the species as threatened: *Rapidophyllum hystrix* and *Smilax smallii*. None of the species found at Morningside are listed as threatened plants by the Florida Natural Areas Inventory (2002), but two are listed as "U.S. management concerns:" *Pteroglossaspis ecristata* and *Verbesina heterophylla*.

Nine species found at Morningside were found to be near or at the northern or southern limits of their geographic range (Wunderlin and Hansen 2003). Two species were found to be at their extreme southern limit in Alachua County: *Pogonia divaricata* and *Agalinis purpurea*. Species that are near their southern limit are: *Aleurites fordii*, *Andropogon gerardii*, and *Pycnanthemum nudum*. *Aleurites fordii* is naturalized and occurs randomly, but is near its southern limit except for a disjunct population in Citrus County. *Andropogon gerardii* and *P. nudum* are at their southern limit in Volusia County. Several species are near their northern limit in Alachua County: *Aristida gyrans*, *Asimina reticulata*, *Chrysopsis scabrella*, and *Solidago odora* var. *chapmanii*. *Aristida gyrans* is at its northern limit in Clay County, *Asimina reticulata* in Bradford County, and *C. scabrella* and *S. odora* var. *chapmanii* in Columbia County. *Chrysopsis subulata* and *Callisia*

ornata are at their northern limit except for a disjunct population of *C. ornata* that occurs in the panhandle (in Gulf County). *Verbesina heterophylla* is at its western limit in Alachua County.

There were 71 species found in the park that are not native to North America north of Mexico but are considered to be naturalized in Florida (Wunderlin 1998). These species are indicated in the Appendix by an asterisk.

PLANT COMMUNITIES

There are five distinct plant communities at Morningside, as determined from community descriptions in Myers and Ewel 1990. These are pine flatwoods, flatwoods depressions, sandhills, cypress swamps, and various ruderal sites. The four ecosystems are very common in Florida, and each has distinct species of plants and animals, as well as characteristic soil and hydrologic conditions.

At Morningside, prescribed fire is an important management tool and is used on a regular basis to maintain the health of the pine flatwoods and sandhills. This fire schedule keeps weedy species and fast-growing hammock shrubs and trees from invading these plant communities.

Pine flatwoods. Pine flatwoods is the most common plant community found in Florida, covering approximately 50 percent of the land in the state. This percentage was probably greater in the past, but due to habitat destruction, resulting from conversion of land to agricultural purposes, forestry operations, and urban growth, the amount of land covered by undisturbed flatwoods has been significantly reduced (Myers and Ewel 1990; Taylor 1998). This community is also the major constituent of Morningside Nature Center, covering 53.6% of the park (Figures 2, 3).

The occurrence of flatwoods in Florida can be explained by past changes in sea level due to the repeated periods of glaciation that may have begun as early as the Miocene period. When the polar ice caps advanced, large areas of the continental shelf were exposed. Then when the ice caps receded, the sea levels rose and these exposed areas were covered with water. During this time, sand was deposited on these shelves. This sandy soil, along with the low elevation of the land and poor drainage, became the necessary ingredients for the formation of today's flatwoods communities (Myers and Ewel 1990).

Pine flatwoods are characterized by a low elevation and flat topography with acidic, sandy soils that are poorly drained, often

Figure 2. Map of Morningside Nature Center, with delimited plant communities.

underlain by a clay hardpan. The sand is underlain by a compressed organic layer formed by the downward movement of organics as water percolates down through the surface. A hardpan, or a compressed layer of clay often underlies this organic layer. The hardpan is formed in a similar fashion. As water percolates through the soil surface, clay and other fine particles and minerals collect beneath the compressed organic layer, forming the hardpan. The soil is usually fine textured, contains few nutrients, and has very low amounts of clay and organic matter (Myers and Ewel 1990).

During the rainy season, water sometimes stands in flatwoods if a hardpan is present, and water depth exceeds the depth of the soil. In contrast, during the dry season, the sandy soil remains extremely dry because there is not enough water present to reach the surface. Therefore, a droughty condition usually persists during such periods. Any organic material that falls to the ground may lessen the effects of drought and high temperatures. It has been found that moisture levels are much higher

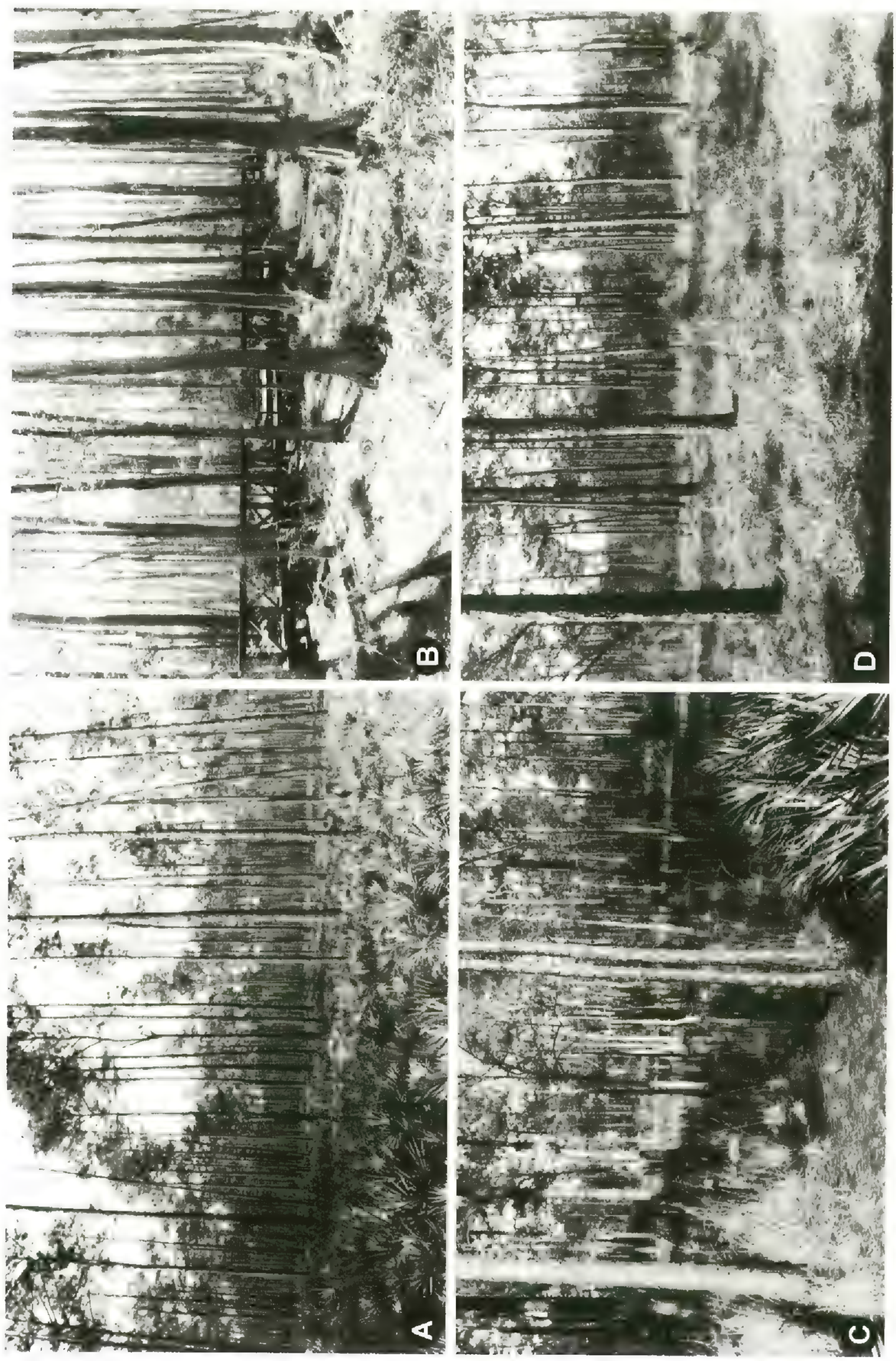

Figure 3. Plant Communities at Morningside Nature Center. A. pine flatwoods. B. cypress swamp. C. flatwoods depression. D. sandhill.

in areas that have not been burned, due to the higher amount of organic litter remaining on the ground (Myers and Ewel 1990).

In the past, natural fires frequently burned flatwoods at one to four year intervals. However, the early settlements of Spanish, followed by English and American settlements in the area, led to a dramatic decrease in the frequency of natural fires. Settlers began farming and also brought livestock to the land; the population increased, which led to the need for roads. These roads and other human constructions acted as barriers to the natural fires, thus causing a decrease in fire frequency. The lack of fire changed the understory of the flatwoods ecosystem, reducing the abundance of herbs, and increasing the dominance of shrubs. It is thought that today's flatwoods are quite different than those of the past, although precise floristic changes are difficult to determine (Myers and Ewel 1990).

The dominant tree species found in flatwoods in Florida are *Pinus palustris*, *P. serotina*, *P. elliottii*, *P. taeda*, *Quercus virginiana*, *Q. nigra*, *Liquidambar styraciflua*, and *Acer rubrum*. Depending on the topology of the area, only one of these pine species may be dominant in any particular place. *Pinus palustris* (longleaf pine) is more fire tolerant than *P. serotina* and *P. elliottii* and is found in higher elevation areas, where there is very rarely standing water at any time of the year. *Pinus elliottii* and *P. serotina* are found in lower elevation areas where water is more prevalent during the rainy season. *Pinus palustris* historically dominated flatwoods, but commercial logging has long since destroyed most of the virgin longleaf pine flatwoods. Because of this logging and suppression of natural fires, all three species of pine are commonly found coexisting in the same area (Myers and Ewel 1990). Commonly, a fourth species of pine, *P. taeda*, also can be found dominating the canopy of the flatwoods. This pine is very fast-growing (Taylor 1998) and quickly colonizes areas that have been disturbed. *Pinus palustris* and *P. elliottii* are the dominant pines in the flatwoods at Morningside (Johnson 1998).

The shrub layer of the flatwoods at Morningside is dominated by *Bejaria racemosa*, *Callicarpa americana*, *Gaylussacia dumosa*, *G. nana*, *Hypericum hypericoides*, *H. tetrapetalum*, *Ilex coriacea*, *I. glabra*, *Kalmia hirsuta*, *Licania michauxii*, *Lyonia lucida*, *Myrica cerifera*, *Quercus minima*, *Q. pumila*, *Rhus copallina*, *Serenoa repens*, and *Vaccinium myrsinites*.

The ground layer consists of a variety of wildflowers and herbaceous species. Dominants include *Aristida stricta* var. *beyrichiana*, *Asclepias pedicellata*, *Carphephorus paniculatus*, *Cirsium horridulum*, *Elephantopus elatus*, *Eupatorium mohrii*, *E. rotundifolium*, *Fuirena scirpoidea*,

Gamochaeta falcata, *Lachnocaulon anceps*, *Oclemena reticulata*, *Polygala nana*, *Pseudognaphalium obtusifolium*, *Pterocaulon pycnostachyum*, *Smilax auriculata*, and *Symphyotrichum walteri*.

Flatwoods depression. The flatwoods depressions, also called flatwoods ponds, depression marshes, or pineland depressions, comprise about 0.4% of the park (Figures 2, 3). These small, shallow, rounded depressions support a unique assemblage of plants due to the ephemeral presence of water. A depression marsh is usually formed when sand slumps over or around a sinkhole and creates a conical depression, which becomes filled by direct rainfall, runoff, or seepage from upland habitats. The soil in these marshes is usually acidic and the center of the depression becomes filled with peat. Fire is important for exclusion of shrubs and trees, and the maintenance of peat. The hydrology of these areas is variable, with most of the depression marshes drying in most years. *Cephalanthus occidentalis* and *Myrica cerifera* are common shrubs found in the depression marshes at Morningside. Typical herbs found in this habitat include: *Agalinis linifolia*, *Lachnanthes caroliniana*, *Pluchea rosea*, *Sagittaria graminea*, *Woodwardia virginica*, and *Xyris caroliniana*.

Sandhill. Sandhills, often called high pinelands, are another common type of community in Florida. Sandhills comprise 21.5% of Morningside (Figures 2, 3). Sandhills are characterized by an open canopy of *Pinus palustris* on rolling sand hills with an open, herb-dominated understory (Johnson 1998; Myers and Ewel 1990). Sandhills were once a very common plant community stretching throughout the southeastern United States from Virginia to eastern Texas. Historically, they provided a great highway through which the early settlers could drive their wagons because of the open canopy and understory (Myers and Ewel 1990).

Like flatwoods, sandhills are fire controlled. Sandhills consist of a unique and varying balance of fire-resistant species that have adapted to the natural fires that sweep through the environment. The life forms in this community are adapted to low-intensity fires that usually occur every one to ten years. Sandhills often grade into other community types such as flatwoods or scrub, and therefore often have many species in common with other plant communities (Myers and Ewel 1990). In fact, it has been hypothesized that presettlement longleaf pine forests occurred on both sandhills and flatwoods. Pollen evidence has shown that the ratio of pines relative to hardwoods in this community has varied over the past 20,000 years. The cause of this fluctuation, however, is still

unknown. The establishment of xeric, fire-adapted species is thought to have greatly increased in the sandhill communities within the last several thousand years. It may have been due to an increase in the frequency of fire, brought about by the agriculture of the Native Americans or an increase in lightning-set fires (Myers and Ewel 1990).

Sandhill formation began as early as the Pleistocene, as ridges possessing coarse, well-drained sands developed. There is much variation in texture, drainage, and fertility of the soil, and because of this variation, it is thought that fire, rather than soil, has been the greatest influence on the patterns of vegetation found in this community. The sand has been derived from marine fluvial deposits and is very low in nutrients (Myers and Ewel 1990).

The vegetation of sandhills consists of a pine canopy, a deciduous oak canopy, and a herbaceous ground cover. Longleaf pine, *Pinus palustris*, is the major overstory species of sandhills. Because of extensive misuse of the land, the virgin longleaf pine forests have been virtually eradicated. This pine is extremely long-lived, reaching ages of more than 500 years. This species is highly fire-resistant and depends on low-intensity fires for its success in the sandhill ecosystem. The trees depend on fire to clear the herbaceous understory, providing bare soil needed for germination. Once a seed germinates, the young tree begins its life as a "grass stage." At this stage, the sapling can easily survive if a fire passes through the area. The apical meristem stays close to the ground and is protected by long, moisture-filled needles. During this period, the sapling builds a long, thick taproot, which stores the water and nutrients the tree will need when it bolts up as a single-stemmed young tree. Rapid bolting soon raises the terminal bud above the fire-level, an advantage if a fire passes through. When the tree is mature, the bark consists of plates, which can flake off when heated in a fire. This dissipates the heat, which protects the trunk from fire damage (Myers and Ewel 1990).

Other common trees found in the sandhill at Morningside include *Quercus incana* and *Q. laevis*. As fire becomes more infrequent, *Diospyros virginiana* becomes frequent. Common shrubs found in sandhills at Morningside include *Asimina angustifolia*, *A. incana*, *A. reticulata*, *Licania michauxii*, *Quercus pumila*, *Rhus copallina*, *Vaccinium myrsinites*, and *V. stamineum*. The understory of the sandhill communities at Morningside include the following herbaceous elements: *Andropogon gyrans*, *Aristida stricta* var. *beyrichiana*, *Balduina angustifolia*, *Berlandiera subacaulis*, *Carphephorus corymbosus*, *Chrysopsis scabrella*, *Cnidoscolus stimulosus*, *Crotolaria rotundifolia*, *Croton argyranthemus*, *Cuthbertia ornata*, *Helianthemum corymbosum*,

Liatris gracilis, *L. pauciflora*, *Opuntia humifusa*, *Palafoxia integrifolia*, *Pityopsis graminifolia*, *Pteridium aquilinum*, *Rhyncospora megalocarpa*, *Rubus cuneifolius*, *Solidago odora* var. *chapmanii*, *Sorghastrum secundum*, *Sporobolus junceus*, and *Stillingia sylvatica*.

The presence of wire grass, *Aristida stricta* var. *beyrichiana*, indicates the health of the sandhill (Myers and Ewel 1990). It is a bunch grass that flourishes under the appropriate conditions and frequent fires. When these conditions are met, the grass forms a dense, vast groundcover. However, many stands of this grass have been eliminated since human settlement. Wire grass spreads very slowly and has actually never been observed creeping into a cleared area, nor does it recolonize an area after being removed. It is also very easily exterminated. It apparently does not frequently grow from seed and often does not even flower. Controlled burning practices are often limited to the winter months, and this fire regime always results in flowering without the production of seed in the wiregrass. It has been found that if the land is burned during the growing season, the grass flowers profusely and produces seed (Myers and Ewel 1990). Therefore, burning regimes should be altered on public and private lands to accommodate this ecologically significant and slowly reproducing species. Fire frequency, intensity, and the season of the fire has profound effects on most species of the sandhill ecosystem. Fire can stimulate seed germination and maintain the understory, but, if not regular, it can also destroy pines and other important species.

Cypress swamp. Cypress swamps encompass approximately 4.4% of the park (Johnson 1998; Figures 2, 3). This ecosystem is the most common type of still-water swamp in Florida, and gets its water supply from shallow, acid groundwater. Such swamps occur in depressions and are usually scattered in poorly drained pine flatwoods. The impermeable clay that underlies the pine flatwoods also underlies the swamp. The rate of decomposition in the swamp is low, and peat accumulates in the depressions. The amount of accumulated organic matter is usually greater than one meter. The water level in these swamps fluctuates greatly, exposing the peat bottom for weeks or even months. Organic acids accumulate in the water, giving it a reddish-brown color, making it impenetrable to light. As a result, phytoplankton cannot survive, which causes the productivity and oxygen level of the swamp to be very low. Fire frequency is moderate and occurs approximately five times per century in a typical cypress swamp. It is thought that these fires burn accumulated organic matter and keep the swamps from becoming mesic ecosystems (Myers and Ewel 1990).

Because of the effects of inundation of the land by water, the plants that grow in the cypress swamps must be able to adapt to the low oxygen and high acid content. As a result, the diversity of these ecosystems is somewhat lower than that of ecosystems that do not have standing water. Also, the diversity found in an area is directly proportional to the amount of time that area is covered by water. The longer an area is submerged, the fewer the number of species that can survive the length of time spent inundated. Having thickened leaves and low transpiration rates are common adaptations for plants living in this ecosystem (Myers and Ewel 1990). Common trees and shrubs found in the cypress swamps at Morningside include: *Acer rubrum*, *Cephalanthus occidentalis*, *Ilex cassine*, *Itea virginica*, *Lyonia lucida*, *Nyssa sylvatica* var. *biflora*, and *Taxodium ascendens*. Common understory herbs are: *Amphicarpum muhlenbergianum*, *Cladium jamaicense*, *Eleocharis vivipara*, *Lachnanthes caroliana*, *Lycopus rubellus*, *Panicum hemitomon*, *Rubus argutus*, *Saururus cernuus*, and *Woodwardia virginica*.

Ruderal. The ruderal habitats roughly cover 20.1% of the park (Figure 2). There are many different disturbed areas at Morningside. For example, the garden near the homestead provides an excellent opportunity for annual weedy species to thrive. The garden is seasonally planted and lays fallow otherwise. Fast-growing species are able to colonize the site. Also, there are many characteristic disturbed or "weedy" species found along the trails, disturbed stream banks, University Avenue and the entrance road, the parking lots, and along the southeast side of the park where the property is adjacent to a housing community. Common trees, shrubs, and vines found in these ruderal areas include *Aleurites fordii*, *Aralia spinosa*, *Cinnamomum camphora*, *Ligustrum lucidum*, *Prunus serotina*, *Sapium sebiferum*, and *Vitis rotundifolia*. Commonly found herbs are *Allium canadense*, *Ambrosia artemisiifolia*, *Cenchrus echinatus*, *Chenopodium ambrosioides*, *Conyza canadensis* var. *pusilla*, *Cyperus croceus*, *Dactyloctenium aegyptium*, *Dioscorea bulbifera*, *Eremochloa ophiuroides*, *Erigeron quercifolius*, *Eupatorium compositifolium*, *Euphorbia cyathophora*, *Paspalum notatum*, *Phytolacca americana* var. *rigida*, *Richardia brasiliensis*, *Setaria parviflora*, *Sida rhombifolia*, *Sporobolus indicus* var. *indicus*, *Stenotaphrum secundatum*, *Wisteria sinensis*, and *Youngia japonica*.

A creek runs along the west side of the park. This area is considered to be ruderal because of constant disturbance caused by dredging the canal. This creek has many dominant species that are unique to this area, including *Cicuta maculata*, *Colocasia esculenta*, *Ludwigia decurrens*,

L. peruviana, *Lygodium japonicum*, *Sesbania punicea*, *Thelypteris hispidula*, and *T. palustris*.

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APPENDIX

ANNOTATED LIST OF SPECIES OF MORNINGSIDE NATURE CENTER

Species nomenclature follows Wunderlin (1998) and the ISB Atlas of Florida Vascular Plants (Wunderlin and Hansen 2003). Nomenclature and circumscription of plant families are based on the APG II (Angiosperm Phylogeny Group 2003) and Judd et al. (2002). Recent taxonomic revisions were also cited for several species. When these recent revisions differed from the taxonomy and nomenclature of Wunderlin (1998), the most recent name was used, and the reference is cited after the species listing.

The species list is arranged alphabetically by family, genus, and species within larger monophyletic groups of ferns, conifers, and angiosperms. Each entry includes the species name, followed by the author or authors (as taken from Wunderlin 1998; Wunderlin and Hansen 2003), the habitat in which it was found, its relative abundance, and the collection number. Collection numbers are those of the first author, with the

assistance of S. Kabat and T. Touchton, unless indicated otherwise. All vouchers listed are housed in FLAS. The communities are: pine flatwoods (PF), flatwoods depression (FD), cypress swamp (CS), sandhill (SH), and ruderal (RU). For abundance, the following categories were used, and were based on the collector's observations of the plants: rare (R; one or very few occurrences), occasional (O; sporadic occurrence), frequent (F; widespread throughout study area or plant community), and common (C; dominants in the plant community). An asterisk (*) indicates non-native taxa that are considered to be naturalized, according to Wunderlin 1998.

FERNS

OSMUNDACEAE. *Osmunda cinnamomea* L. – CS; C; *309*. *Osmunda regalis* L. var. *spectabilis* (Willd.) A. Gray – CS, RU; O; *526*.

POLYPODIACEAE (including Aspleniaceae, Blechnaceae, Dennstaedtiaceae, and Thelypteridaceae, etc.; Judd et al. 2002; Pryer et al. 1995; Saulmon 1971). *Asplenium platyneuron* (L.) Britton et al. – RU; O; *369*. *Pteridium aquilinum* (L.) Kuhn var. *pseudocaudatum* (Clute) A. Heller - PF, SH; C; *270*. *Thelypteris hispidula* (Decne.) C.F. Reed var. *versicolor* (R.P. St. John) Lellinger – RU; O; *371*. *Thelypteris palustris* Schott var. *pubescens* (G. Lawson) Fernald – RU; O; *145*. *Woodwardia areolata* (L.) T. Moore – CS, FD, RU; F; *236*. *Woodwardia virginica* (L.) Sm. – CS, FD; F; *204*, *217*, *245*.

SCHIZAEACEAE. **Lygodium japonicum* (Thunb.) Sw. – RU; F; *367*.

CONIFERS

CUPRESSACEAE (including Taxodiaceae, Judd et al. 2002; Watson 1993). *Juniperus virginiana* L. – RU; O; *289*. *Taxodium ascendens* Brongn. – CS; F; *364*, *626*.

PINACEAE. *Pinus elliottii* Engelm. – PF; C; *493*. *Pinus palustris* Mill. – SH; C; *265*. *Pinus taeda* L. – RU, SH; F; *220*, *365*.

ANGIOSPERMS

ACANTHACEAE. *Dyschoriste oblongifolia* (Michx.) Kuntze – SH; O; *33*, *489a*. *Ruellia caroliniensis* (J.F. Gmel.) Steud. – RU; R; *489b*.

ADOXACEAE. *Sambucus nigra* L. subsp. *canadensis* (L.) Bolli – RU; R; *465*. *Viburnum nudum* L. – PF; O; *354*.

AGAVACEAE. *Yucca aloifolia* L. – RU; O; *538*.

ALISMATACEAE. *Sagittaria graminea* Michx. var. *graminea* – CS, FD, PF; O; *135*, *239*, *608*.

ALLIACEAE. *Allium canadense* L. var. *canadense* – RU; F; *523*.

ALTINGIACEAE. *Liquidambar styraciflua* L. – CS, RU; C; *485*.

AMARANTHACEAE (including Chenopodiaceae). **Alternanthera philoxeroides* (Mart.) Griseb. – RU; C; *142*. **Amaranthus viridis* L. – RU; R; *L.J. Lehtonen 456*. **Chenopodium ambrosioides* L. – RU; C; *254*.

AMARYLLIDACEAE. *Zephyranthes atamasca* (L.) Herb. var. *treatiae* (S. Watson) Meerow – CS; O; *447*.

ANACARDIACEAE. *Rhus copallinum* L. – PF, SH; C; *148*. *Toxicodendron radicans* (L.) Kuntze – RU; C; *190*.

ANNONACEAE. *Asimina angustifolia* Raf. – PF, SH; C; *41, 59, 160*. *Asimina angustifolia* Raf. × *A. incana* (W. Bartram) Exell. – SH; O; *653*. *Asimina incana* (W. Bartram) Exell. – PF, SH; F; *15*. *Asimina pygmaea* (W. Bartram) Dunal – SH; O; *161*. *Asimina reticulata* Shuttlew. *ex* Chapm. – PF; O; *285*.

APIACEAE (including Araliaceae; Judd et al. 2002). *Aralia spinosa* L. – RU; F; *475*. *Centella asiatica* (L.) Urb. – RU; O; *472*. *Cicuta maculata* L. – RU; O; *141*. **Cyclospermum leptophyllum* (Pers.) Sprague *ex* Britton & P. Wilson – RU; F; *423, 550*. *Eryngium aromaticum* Baldwin – SH; O; *206*. *Eryngium baldwinii* Spreng. – PF, RU; O; *80, 528*. *Eryngium yuccifolium* Michx. – PF, SH; O; *83*. *Hydrocotyle umbellata* L. – RU; O; *442*. *Hydrocotyle verticillata* Thunb. – RU; R; *L.J. Lehtonen 206*. *Oxypolis filiformis* (Walter) Britton subsp. *filiformis* – PF; R; *L.J. Lehtonen 358*. *Ptilimnium capillaceum* (Michx.) Raf. - PF; R; *L.J. Lehtonen 280, 541*. *Spermolepis divaricata* (Walter) Raf. – RU; F; *488*.

APOCYNACEAE (including Asclepiadaceae). *Asclepias amplexicaulis* Sm. – SH; O; *498b*. *Asclepias cinerea* Walter – SH; O; *63*. *Asclepias humistrata* Walter – SH; O; *2, 498a*. *Asclepias longifolia* Michx. – PF; R; *501, 552*. *Asclepias pedicellata* Walter – PF; F; *180*. *Asclepias tuberosa* L. – PF, SH; O; *37*. *Asclepias verticillata* L. – PF, SH; O; *112, 150*.

AQUIFOLIACEAE. *Ilex cassine* L. – CS, PF; O; *133*. *Ilex coriacea* (Pursh) Chapm. – CS; O; *312*. *Ilex glabra* (L.) A. Gray – PF; C; *44*. *Ilex opaca* var. *opaca* Aiton – CS, PF; O; *215*. *Ilex vomitoria* Aiton – PF; O; *340*.

ARACEAE (including Lemnaceae). **Colocasia esculenta* (L.) Schott – RU; C; *370*. *Lemna aequinoctialis* Welw. – CS, FD; C; *410*.

ARECACEAE. **Butia capitata* Becc. – RU; R; *500*. *Rhapidophyllum hystrix* (Pursh) H. Wendl. & Drude *ex* Drude – RU; R; *337*. *Sabal palmetto* (Walter) Lodd. *ex* Schult. & Schult. f. – PF, RU, SH; O; *444*. *Serenoa repens* (W. Bartram) Small – PF; C; *87*.

ASTERACEAE. *Acmella oppositifolia* (Lam.) R.K. Jansen var. *repens* (Walter) R.K. Jansen – RU; O; *404*. *Ageratina jucunda* (Greene) Clewell & Wooten – SH; C; *382*. *Ambrosia artemisiifolia* L. – RU; F; *392*. *Arnoglossum floridanum* (A. Gray) H. Rob. – SH; F; *115*. *Baccharis halimifolia* L. – RU, SH; O; *293*. *Balduina angustifolia* (Pursh) B.L. Rob. – SH; O; *28, 130, 223*. *Berlandiera subacaulis* (Nutt.) Nutt. – SH; F; *27*. *Bidens alba* (L.) DC. var. *radiata* (Sch. Bip.) R.E. Ballard *ex* Melchert. – RU; F; *54*.

Bidens laevis (L.) Britton et al. – RU; O; *405*. *Bidens mitis* (Michx.) Sherff – CS, RU; F; *363, 377*. *Carphephorus corymbosus* (Nutt.) Torr. & A. Gray – SH; C; *250*. *Carphephorus odoratissimus* (J.F. Gmel.) H. Hebert – PF; F; *240*. *Carphephorus paniculatus* (J.F. Gmel.) H. Hebert – PF; F; *386*. *Chaptalia tomentosa* Vent. – PF; R; *415*. *Chrysopsis mariana* (L.) Elliott – SH; O; *101, 362*. *Chrysopsis scabrella* Torr. & A. Gray – SH; C; *251*. *Chrysopsis subulata* Small – PF; F; *247, 301*. *Cirsium horridulum* Michx. – PF, RU; F; *483*. *Cirsium nuttallii* DC. – RU; R; *77*. *Conyza canadensis* (L.) Cronquist var. *pusilla* (Nutt.) Cronquist – RU; O; *255, 276*. *Eclipta prostrata* (L.) L. – RU; O; *598*. *Elephantopus elatus* Bertol. – PF, RU, SH; C; *172*. *Elephantopus nudatus* A. Gray – SH; O; *366*. **Emilia fosbergii* Nicolson – RU; R; *651*. *Erechtites hieracifolia* (L.) Raf. *ex* DC. – CS; C; *99*. *Erigeron quercifolius* Lam. – RU; C; *31, 431*. *Erigeron strigosus* Muhl. *ex* Willd. – FD, RU; R; *543*. *Erigeron vernus* (L.) Torr. & A. Gray – PF, RU; O; *102, 619*. *Eupatorium capillifolium* (Lam.) Small – RU, SH; F; *281*. *Eupatorium compositifolium* Walter – PF, RU, SH; C; *307*. *Eupatorium mohrii* Greene – PF; O; *76, 134, 177*. *Eupatorium pilosum* Walter – PF; O; *233*. *Eupatorium rotundifolium* L. – PF; F; *242*. *Euthamia caroliniana* (L.) Greene *ex* Porter & Britton – PF, RU, SH; F; *343*. *Gamochaeta falcata* (Lam.) Cabrera – PF; O; *486* (Wunderlin and Hansen 2003). *Gamochaeta pensylvanica* (Willd.) Cabrera – RU; O; *21* (Wunderlin and Hansen 2003). *Helianthus angustifolius* L. – PF; O; *237, 590*. *Helianthus radula* (Pursh) Torr. and A. Gray – SH; O; *199*. *Hieracium gronovii* L. – PF, SH; C; *192, 195*. *Hieracium megacephalon* Nash – SH; O; *34, 108*. *Krigia virginica* (L.) Willd. – RU; O; *458*. *Lactuca canadensis* L. – PF; R; *L.J. Lehtonen 390*. *Lactuca graminifolia* Michx. – RU; F; *114, 514*. *Liatris gracilis* Pursh – SH; C; *300*. *Liatris pauciflora* Pursh – SH; C; *225*. *Liatris tenuifolia* Nutt. var. *tenuifolia* – SH; C; *269*. *Lygodesmia aphylla* (Nutt.) DC. – SH; O; *24*. *Melanthera nivea* (L.) Small – RU; R; *227*. *Mikania scandens* (L.) Willd. – RU; O; *368*. *Oclemena reticulata* (Pursh) Greene – PF; R; *502, 574* (Wunderlin and Hansen 2003). *Palafoxia integrifolia* (Nutt.) Torr. & A. Gray – SH; C; *249*. *Pityopsis graminifolia* (Michx.) Nutt. – SH; C; *197*. *Pluchea odorata* (L.) Cass. – FD; R; *L.J. Lehtonen 342*. *Pluchea rosea* R.K. Godfrey – FD; R; *92, 246*. *Pseudognaphalium obtusifolium* (L.) Hillard & B.L. Burtt – PF; O; *221* (Wunderlin and Hansen 2003). *Pterocaulon pycnostachyum* (Michx.) Elliott – PF, RU; C; *29*. *Pyrrhopappus carolinianus* (Walter) DC. – RU; F; *539, 544*. *Rudbeckia hirta* L. – SH; R; *L.J. Lehtonen 308*. *Sericocarpus tortifolius* (Michx.) Nees – PF, SH; C; *241* (Wunderlin and Hansen 2003). *Solidago fistulosa* Mill. – PF; O; *375, 409*. *Solidago odora* Aiton var. *chapmanii* (Torr. & A. Gray) Cronquist – SH; C; *147, 193*. *Solidago stricta* Aiton – PF; R; *L.J. Lehtonen 393*. *Solidago tortifolia* Elliott – SH; F; *268*. **Sonchus oleraceus* L. – RU; F; *422, 516*. *Symphyotrichum adnatum* (Nutt.) G.L. Nesom – SH; O; *611* (Wunderlin and Hansen 2003). *Symphyotrichum concolor* (L.) G.L. Nesom – SH; O; *413* (Wunderlin and Hansen 2003). *Symphyotrichum dumosum* (L.) G.L. Nesom – PF, RU, SH; C; *391* (Wunderlin and Hansen 2003). *Symphyotrichum walteri* (Alexander) G.L. Nesom – PF; F; *243* (Wunderlin and Hansen 2003). *Verbesina heterophylla* (Chapm.) A. Gray – SH; O; *113, 579*. *Vernonia angustifolia* Michx. – SH; R; *L.J. Lehtonen 310*. **Youngia japonica* (L.) DC. – RU; O; *381*.

BEGONIACEAE. **Begonia cucullata* Willd. – RU; O; *139*.

BIGNONIACEAE. *Campsis radicans* (L.) Seemann *ex* Bureau – PF; O; *89*.

BRASSICACEAE. *Descurainia pinnata* (Walter) Britton – RU; C; *427. Lepidium virginicum* L. – RU; O; *14. *Raphanus raphanistrum* L. – RU; O; *56.*

BROMELIACEAE. *Tillandsia bartramii* Elliott – RU; R; *681. Tillandsia recurvata* (L.) L. – PF, RU; F; *278. Tillandsia usneoides* (L.) L. – PF, RU; C; *264.*

CACTACEAE. *Opuntia humifusa* (Raf.) Raf. – SH; F; *511.*

CAMPANULACEAE. *Lobelia glandulosa* Walt. – PF; O; *387. Lobelia paludosa* Nutt. – PF; O; *45, 189. Triodanis perfoliata* (L.) Nieuwl. – RU; O; *434. *Wahlenbergia marginata* (Thunb.) A. DC. – SH; R; *19, 105.*

CANNABACEAE (Judd et al. 2002, as Celtidaceae; Stevens 2002). *Celtis laevigata* Willd. – PF; O; *346.*

CANNACEAE. *Canna flaccida* Salisb. – CS; F; *74, 577.*

CAPRIFOLIACEAE. **Lonicera japonica* Thunb. – RU; O; *283, 622. Lonicera sempervirens* L. – RU; O; *482.*

CARYOPHYLLACEAE. *Arenaria serpyllifolia* L. subsp. *serpyllifolia* – RU; O; *457b. Drymaria cordata* (L.) Willd. *ex* Schult. – RU; O; *468. Silene antirrhina* L. – RU; F; *545. *Stellaria media* (L.) Vill. – RU; F; *457a.*

CHRYSOBALANACEAE. *Licania michauxii* Prance – SH; C; *51.*

CISTACEAE. *Helianthemum carolinianum* (Walter) Michx. – PF, SH; O; *649, L.J. Lehtonen 223a. Helianthemum corymbosum* Michx. – SH; O; *58. Lechea minor* L. – SH; F; *299. Lechea mucronata* Raf. – SH; O; *127. Lechea pulchella* Raf. – PF; R; *L.J. Lehtonen 336. Lechea sessiliflora* Raf. – SH; O; *152, 459. Lechea torreyi* (Chapm.) Legg. *ex* Britton – PF; O; *451.*

CLUSIACEAE (including Hypericaceae; Judd et al. 2002). *Hypericum brachyphyllum* (Spach) Steud. – PF; R; *645. Hypericum cistifolium* Lam. – PF; O; *376. Hypericum crux-andreae* (L.) Crantz – PF; O; *201. Hypericum gentianoides* (L.) Britton et al. – SH; R; *L.J. Lehtonen 309. Hypericum hypericoides* (L.) Crantz – PF; F; *151, 174, 183. Hypericum mutilum* L. – RU; F; *562. Hypericum myrtifolium* Lam. – PF; O; *70. Hypericum tetrapetalum* Lam. – FD, PF; O; *187.*

COMMELINACEAE. *Callisia ornata* (Small) G.C. Tucker – SH; C; *40. *Commelina benghalensis* L. – RU; R; *257. Commelina erecta* L. – RU, SH; O; *36, 230. *Murdannia nudiflora* (L.) Brenan – RU; F; *594. Tradescantia ohiensis* Raf. – RU; R; *88, 229.*

CONVOLVULACEAE. *Cuscuta compacta* Juss. *ex* Choisy – PF; O; *356. Dichondra carolinensis* Michx. – RU; F; *315. Ipomoea cordatotriloba* Dennst. – RU; F; *274. Ipomoea pandurata* (L.) G. Meyer – SH; O; *117. *Ipomoea quamoclit* L. – RU; O; *252. Ipomoea* cf. *sagittata* Poir. – RU; R; *643. *Merremia dissecta* (Jacq.) Hallier f. – RU; R; *121. Stylisma patens* (Desr.) Myint – SH; O; *131.*

CORNACEAE (including Nyssaceae). *Cornus florida* L. – RU (possibly planted); O; *479. Nyssa sylvatica* Marshall var. *biflora* (Walter) Sarg. – CS, FD; C; *316, 606.*

CUCURBITACEAE. *Melothria pendula* L. – RU; O; *186.*

CYPERACEAE. **Bulbostylis barbata* (Rottb.) C.B. Clarke – RU; C; *164. Bulbostylis stenophylla* (Elliott) C.B. Clarke – RU; C; *157. Bulbostylis warei* (Torr.) C.B. Clarke – SH; F; *129. Carex elliottii* Schwein. & Torr. – RU; O; *530. Carex longii* Mack. – RU; R; *437, 563. Carex lupulina* Muhl. *ex* Willd. – RU; O; *525. Carex verrucosa* Muhl. – PF; F; *176. Cladium jamaicense* Crantz – CS; C; *553. Cyperus compressus* L. – RU; C; *166, 212a. Cyperus croceus* Vahl – RU; C; *23, 154, 208. Cyperus cuspidatus* Kunth – RU; O; *212b. Cyperus distinctus* Steud. – RU; O; *143. Cyperus filiculmis* Vahl – RU; O; *159b. Cyperus polystachyos* Rottb. – RU; C; *162. Cyperus retrorsus* Chapm. – RU; C; *104, 155, 159a, 211. Cyperus strigosus* L. – RU; O; *402. Eleocharis tuberculosa* (Michx.) Roem. & Schult. – RU; O; *529a. Eleocharis vivipara* Link – CS; C; *101, 557. Fimbristylis autumnalis* (L.) Roem. & Schult. – RU; R; *165. Fimbristylis caroliniana* (Lam.) Fernald – PF; R; *L.J. Lehtonen 260. Fuirena scirpoidea* Michx. – PF; F; *491. Kyllinga odorata* Vahl – RU; O; *167, 210.* **Kyllinga squamulata* Thonn. *ex* Vahl – RU; O; *644. Rhynchospora cephalantha* A. Gray – CS; O; *519, 558a. Rhynchospora corniculata* (Lam.) A. Gray – CS; O; *412. Rhynchospora fascicularis* (Michx.) Vahl – CS; F; *73, 188. Rhynchospora megalocarpa* A. Gray – SH; F; *495. Rhynchospora microcarpa* Baldwin *ex* A. Gray – CS; O; *556. Rhynchospora microcephala* (Britton) Britton *ex* Small – RU; R; *470. Rhynchospora wrightiana* Boeck. – CS; O; *558b. Scirpus cyperinus* (L.) Kunth – CS, RU; F; *280, 582. Scleria triglomerata* Michx. – PF; O; *504.*

DIOSCOREACEAE. **Dioscorea bulbifera* L. – RU; F; *218.*

DROSERACEAE. *Drosera brevifolia* Pursh – PF; F; *648.*

EBENACEAE. *Diospyros virginiana* L. – SH; F; *271.*

ERICACEAE. *Bejaria racemosa* Vent. – PF; F; *86. Gaylussacia dumosa* (Andrews) Torr. & A. Gray – SH; F; *9, 48. Gaylussacia nana* (A. Gray) Small – PF; F; *492* (Luteyn et al. 1996). *Gaylussacia tomentosa* (L.) Torr. & A. Gray *ex* Torr. – PF; C; *48* (Luteyn et al. 1996). *Kalmia hirsuta* Walter – PF; F; *84. Leucothoe racemosa* (L.) A. Gray – CS, PF; O; *330a. Lyonia fruticosa* (Michx.) G.S. Torr. – PF; C; *46. Lyonia ligustrina* (L.) DC. var. *foliosiflora* (Michx.) Fernald – PF; O; *559. Lyonia lucida* (Lam.) K. Koch – CS, PF; C; *43, 98, 331. Lyonia mariana* (L.) D. Don – PF; R; *566. Rhododendron viscosum* (L.) Torr. – PF; R; *118. Vaccinium arboreum* Marshall PF, SH; F; *11, 305, 466. Vaccinium corymbosum* L. – PF; F; *284, 330b, 450, 474, 560* [our material included both the *V. fuscatum* Aiton entity (*330b, 474*) and the *V. ashei* (L.) Reade entity (*284, 450, 560, 564*; Uttal 1987)]. *Vaccinium myrsinites* Lam. – PF, SH; C; *426. Vaccinium stamineum* L. – PF, SH; C; *6, 8, 16.*

ERIOCAULACEAE. *Eriocaulon decangulare* L. – PF; F; *71. Lachnocaulon anceps* (Walter) Morong – PF; F; *448. Syngonanthus flavidulus* (Michx.) Ruhland – PF; F; *67, 429.*

EUPHORBIACEAE. *Acalypha gracilens* A. Gray – RU; C; *311*. **Aleurites fordii* Hemsl. – RU; F; *533*. *Chamaesyce hirta* (L.) Millsp. – RU; O; *332*. *Chamaesyce hypericifolia* (L.) Millsp. – RU; R; *407*. *Chamaesyce hyssopifolia* (L.) Small – RU; F; *256, 334, 335*. *Chamaesyce maculata* (L.) Small – RU; F; *333*. *Cnidoscolus stimulosus* (Michx.) Engelm. & A. Gray – RU, SH; C; *477*. *Croton argyranthemus* Michx. – SH; F; *5*. *Croton glandulosus* L. var. *glandulosus* – SH; O; *350*. *Croton michauxii* G.L. Webster – SH; O; *327*. *Euphorbia cyathophora* (Murray) Bartl. – RU; F; *394*. **Sapium sebiferum* (L.) Roxb. – RU; O; *467*. *Stillingia sylvatica* L. – PF, SH; F; *13*. *Tragia urens* L. – SH; O; *38*.

FABACEAE. *Aeschynomene viscidula* Michx. – SH; O; *125*. **Albizia julibrissin* Durazz. – RU; R; *401*. *Baptisia alba* (L.) Vent. – RU; R; *651*. *Centrosema virginianum* (L.) Benth. – SH, RU; O; *52*. *Cercis canadensis* L. – RU; R; *149*. *Chamaecrista fasciculata* (Michx.) Greene – RU; O; *203*. *Chamaecrista nictitans* (L.) Moench var. *nictitans* – SH; C; *194*. *Clitoria mariana* L. – PF, SH; F; *L.J. Lehtonen 250*. **Crotalaria pallida* Aiton var. *obovata* (G. Don) Polhill – RU; O; *219*. *Crotalaria rotundifolia* J.F. Gmel. – PF, RU, SH; C; *3, 22, 66*. *Dalea carnea* (Michx.) Poir. var. *albida* (Torr. & A. Gray) Barneby – SH; R; *D. & G. Place 380*. *Dalea carnea* (Michx.) Poir. var. *carnea* - SH; R; *326*. *Dalea pinnata* (J.F. Gmel.) Barneby var. *pinnata* – SH; C; *260*. *Desmodium ciliare* (Muhl. *ex* Willd.) DC. – SH; O; *341*. *Desmodium floridanum* Chapm. – SH; O; *110, 355*. *Desmodium incanum* DC. – RU; F; *123, 329, 351b*. *Desmodium lineatum* DC. – SH; F; *588*. *Desmodium paniculatum* (L.) DC. – SH; O; *351a*. *Desmodium tenuifolium* Torr. & A. Gray – PF, RU; F; *198*. **Desmodium tortuosum* (Sw.) DC. RU; R; *L. Johnson s.n., 7 Sep 1982*. **Desmodium triflorum* (L.) DC. – RU; F; *548*. *Desmodium viridiflorum* (L.) DC. – RU, SH; O; *171*. *Erythrina herbacea* L. – SH; R; *505*. *Galactia regularis* (L.) Britton et al. – SH; F; *61, 116, 328*. *Galactia volubilis* (L.) Britton – SH; R; *L.J. Lehtonen 320*.**Indigofera hirsuta* L. – RU; F; *258*. **Indigofera spicata* Forssk. – RU; O; *361*. *Lespedeza hirta* (L.) Hornem. – SH; O; *259*. **Medicago lupulina* L. – RU; O; *461*. **Melilotus albus* Medik. – RU; F; *518*. *Mimosa quadrivalvis* L. var. *angustata* (Torr. & A. Gray) Barneby – SH; F; *30*. *Mimosa strigillosa* Torr. & A. Gray – RU; R; *614*. *Pediomelum canescens* (Michx.) Rydb. – SH; O; *7*. *Rhynchosia difformis* (Elliott) DC. – SH; R; *L.J. Lehtonen 460*. *Rhynchosia reniformis* DC. – SH; C; *4b*. *Rhynchosia tomentosa* (L.) Hook. & Arn. var. *tomentosa* – PF, SH; F; *4a, 512*. *Sesbania herbacea* (Mill.) McVaugh – RU; O; *397, 593*. **Sesbania punicea* (Cav.) Benth. – RU; F; *522*. *Stylosanthes biflora* (L.) Britton, Sterns & Pogg. – SH; C; *109*. *Tephrosia chrysophylla* Pursh – SH; O; *302*. *Tephrosia hispidula* (Michx.) Pers. – PF, SH; O; *200, 513*. **Wisteria sinensis* (Sims) Sweet – RU; F; *534*. *Zornia bracteata* J.F. Gmel. – SH; O; *107, 196*.

FAGACEAE. *Quercus ×asheana* Little (*Q. incana × Q. laevis*) – SH; R; *569*. *Quercus falcata* Michx. – RU (planted?); O; *481*. *Quercus geminata* Small – SH; O; *224*. *Quercus hemispherica* W. Bartram *ex* Willd. – SH; F; *128, 222* (Muller 1970). *Quercus incana* W. Bartram – SH; C.; *304, 380a*. *Quercus laevis* Walter – SH; C; *494*. *Quercus laurifolia* Michx. – RU; O; *535*. *Quercus minima* (Sarg.) Small – PF, SH; C; *298*. *Quercus myrtifolia* Willd. - SH; O; *303*. *Quercus nigra* L. – CS, RU; C; *277, 379*. *Quercus pumila* Walter – PF, SH; C; *94*. *Quercus virginiana* Mill. – RU; R; *476, 570*. *Quercus ×walteriana* Ashe (*Q. nigra × Q. laevis*) – SH; R; *288*.

GELSEMIACEAE. *Gelsemium sempervirens* (L.) W.T. Aiton – PF; F; *441*.

GENTIANACEAE. *Sabatia brevifolia* Raf. – PF; O; *604*.

GERANIACEAE. *Geranium carolinianum* L. – RU; R; *455*.

HAEMODORACEAE. *Lachnanthes caroliana* (Lam.) Dandy – CS, FD; C; *575*, *L.J. Lehtonen 366*.

HALORAGACEAE. *Proserpinaca palustris* L. – RU; R; *650*. *Proserpinaca pectinata* Lam. – FD; R; *L.J. Lehtonen 352*.

HYPOXIDACEAE. *Hypoxis juncea* Sm. – PF; F; *65*, *85*, *181*.

IRIDACEAE. *Iris hexagona* Walter – CS; R; *647;* both blue and white floral forms. *Sisyrinchium angustifolium* Mill. – PF; O; *446* [systematics of this group is unclear, and some systematists refer our plants to *S. atlanticum* E.P. Bicknell]. **Sisyrinchium rosulatum* E.P. Bicknell – RU; R; *L.J. Lehtonen 446*.

ITEACEAE. *Itea virginica* L. – CS; F; *97*, *509*.

JUGLANDACEAE. *Carya glabra* (Mill.) Sweet – RU; O; *496*.

JUNCACEAE. *Juncus elliottii* Chapm. – PF, SH; O; *75*, *503*. *Juncus marginatus* Rostk. – PF; O; *126*, *414*. *Juncus megacephalus* M.A. Curtis – RU; O; *421*, *519c*. *Juncus scirpoides* Lam. – PF; O; *185*.

KRAMERIACEAE. *Krameria lanceolata* Torr. – SH; R; *L.J. Lehtonen 447*.

LAMIACEAE. *Callicarpa americana* L. – PF; C; *90*. **Clerodendrum bungei* Steud. – RU; O; *537*. **Clerodendrum indicum* (L.) Kuntze – RU; O; *532*. *Hyptis alata* (Raf.) Shinners – RU; F; *228*, *235*. **Hyptis mutabilis* (Rich.) Briq. – RU; O; *226*, *395*, *424*. **Lamium amplexicaule* L. – RU; R; *454*. *Lycopus rubellus* Moench – CS; C; *214*. **Physostegia virginiana* (L.) Benth. – RU; R; *403*. *Pycnanthemum nudum* Nutt. – PF; R; *607*. *Salvia azurea* Michx. *ex* Lam. – SH; F; *272*. *Salvia lyrata* L. – RU; R; *310*. *Scutellaria integrifolia* L. – PF, SH; F; *344*. *Scutellaria multiglandulosa* (Kearney) Small *ex* R.M. Harper – SH; R; *42*, *238*. *Stachys floridana* Shuttlew. *ex* Benth. – RU; O; *400*. *Trichostema setaceum* Houtt. – SH; O; *248*.

LAURACEAE. **Cinnamomum camphora* (L.) J. Presl – RU; O; *373*. *Persea palustris* (Raf.) Sarg. – CS; C; *96*, *306*, *589*.

LENTIBULARIACEAE. *Pinguicula pumila* Michx. – PF; C; *388*, *417*. *Utricularia juncea* Vahl – PF; C; *389*. *Utricularia purpurea* Walter – FD; O; *617*. *Utricularia subulata* L. – PF; R; *L.J. Lehtonen 253*.

LOGANIACEAE. *Mitreola sessilifolia* (J.F. Gmel.) G. Don – FD; R; *L.J. Lehtonen 335*.

LYTHRACEAE. **Cuphea carthagenensis* (Jacq.) J.F. Macbr. – FD; R; *L.J. Lehtonen 204*.

MAGNOLIACEAE. *Magnolia grandiflora* L. – CS, RU; O; *279, 339*. *Magnolia virginiana* L. – CS; F; *573*.

MALVACEAE. *Sida rhombifolia* L. – RU; O; *393*.

MELANTHIACEAE. *Schoenocaulon dubium* (Michx.) Small – SH; C; *64*.

MELASTOMATACEAE. *Rhexia mariana* L. – PF, RU; F; *91, 95, 580*. *Rhexia nuttallii* C.W. James – PF; R; *L.J. Lehtonen 324*. *Rhexia petiolata* Walter – PF; R; *L.J. Lehtonen 314*.

MOLLUGINACEAE. **Mollugo verticillata* L. – RU; F; *549*.

MORACEAE. **Broussonetia papyrifera* (L.) Vent. – RU; R; *603*.

MYRICACEAE. *Myrica cerifera* L. var. *cerifera* – CS, PF, RU; C; *266* (Clewell 1985). *Myrica cerifera* L. var. *pumila* Michx. – PF; F; *453* (Clewell 1985).

NARTHECIACEAE. *Aletris obovata* Nash *ex* Small – SH; R; *680*.

NYCTAGINACEAE. *Boerhavia diffusa* L. – RU; O; *396*.

OLEACEAE. **Ligustrum lucidum* W.T. Aiton – RU; O; *425*. **Ligustrum sinense* Lour. – RU; O; *419*. *Osmanthus americanus* (L.) Benth. & Hook. f. *ex* A. Gray – PF; R; *561, 616*.

ONAGRACEAE. *Gaura angustifolia* Michx. RU; F; *520*. *Ludwigia decurrens* Walter – RU; O; *398, 399, 620*. *Ludwigia erecta* (L.) H. Hara – RU; R; *599*. *Ludwigia maritima* R.M. Harper – PF; O; *231, 384, 578*. *Ludwigia palustris* (L.) Elliott – PF; R; *357, 487*. **Ludwigia peruviana* (L.) H. Hara RU; O; *294*. *Ludwigia suffruticosa* Walter – RU; R; *L.J. Lehtonen 334, 334a*. *Oenothera laciniata* Hill – RU; F; *517*.

ORCHIDACEAE. *Pogonia divaricata* (L.) R. Br. – PF; R; *L.J. Lehtonen 264*. *Pteroglossaspis ecristata* (Fernald) Rolfe – SH; O; *170*. *Spiranthes vernalis* Engelm. & A. Gray – RU; R; *L.J. Lehtonen 274*.

OROBANCHACEAE. *Agalinis fasciculata* (Elliott) Raf. – PF; R; *L.J. Lehtonen 385*. *Agalinis filifolia* (Nutt.) Raf. – PF; O; *385*. *Agalinis linifolia* (Nutt.) Britton – FD, PF; O; *244*. *Agalinis purpurea* (L.) Pennell – CS; R; *M.S. Carrara 12, L.J. Lehtonen 409*. *Aureolaria pedicularia* (L.) Raf. var. *pectinata* (Nutt.) Gleason – SH; O; *10*. *Buchnera americana* L. – PF; O; *609, L.J. Lehtonen 239, 291*. *Seymeria cassioides* (G.F. Gmel.) S.F. Blake – PF, SH; F; *262*.

OXALIDACEAE. *Oxalis corniculata* L. – RU; O; *57, 624*. **Oxalis debilis* Kunth var. *corymbosa* (DC.) Lourteig – RU; O; *480*.

PAPAVERACEAE (including Fumariaceae). *Corydalis micrantha* (Engelm. *ex* A. Gray) A. Gray – RU; R; *L.J. Lehtonen 424*.

PASSIFLORACEAE. *Passiflora incarnata* L. – RU; O; *527*.

PHYLLANTHACEAE. **Phyllanthus urinaria* L. - RU; O; *408*.

PHYTOLACCACEAE. *Phytolacca americana* L. var. *rigida* Caulkins & Wyatt – RU; F; *531* (Caulkins and Wyatt 1990).

PLANTAGINACEAE. *Bacopa caroliniana* (Walter) B.L. Rob. – FD; R; *L.J. Lehtonen 354*. *Gratiola hispida* (Benth. *ex* Lindl.) Pollard – PF; O; *62, 313*. *Gratiola pilosa* Michx. – PF; R; *L.J. Lehtonen 321*. *Gratiola virginiana* L. – CS; R; *L.J. Lehtonen 435*. *Linaria canadensis* (L.) Chaz. – RU; O; *20, 484*. *Linaria floridana* Chapm. – SH; O; *L.J. Lehtonen 431*. *Penstemon australis* Small – SH; R; *L.J. Lehtonen 219*. *Plantago virginica* L. – RU; C; *435*. *Scoparia dulcis* L. – PF; O; *286, 591*. **Veronica arvensis* L. – RU; R; *456*. *Veronica peregrina* L. – RU; O; *439*.

POACEAE. *Amphicarpum muhlenbergianum* (Schult.) Hitchc. – CS; C; *510*. *Andropogon brachystachyus* Chapm. – PF, RU; R; *317, 634*. *Andropogon gerardii* Vitman – PF; F; *347, 360*. *Andropogon glomeratus* (Walter) Britton, Sterns & Poggenb. var. *glaucopsis* (Elliott) C. Mohr. – PF, SH; C; *342*. *Andropogon glomeratus* (Walter) Britton, Sterns & Poggenb. var. *glomeratus* – PF; F; *636*. *Andropogon glomeratus* (Walter) Britton, Sterns & Poggenb. var. *hirsutior* (Hack.) C. Mohr – PF; O; *132, 631*. *Andropogon glomeratus* (Walter) Britton, Sterns & Poggenb. var. *pumilus* (Vasey) Vasey *ex* L.H. Dewey – RU; F; *273, 627, 633*. *Andropogon gyrans* Ashe var. *gyrans* – SH; F; *383b*. *Andropogon ternarius* Michx. – SH; C; *60, 106*. *Andropogon virginicus* L. var. *glaucus* Hack. – PF; F; *632*. *Andropogon virginicus* L. var. *virginicus* – PF, RU, SH; F; *290, 635, 637, 639*. *Anthaenantia villosa* (Michx.) P. Beauv. – SH; R; *J.R. Abbott 9721*. *Aristida gyrans* Chapm. – SH; O; *318, 319*. *Aristida purpurascens* Poir. var. *tenuispica* (Hitchc.) Allred – PF; O; *629, 630*. *Aristida spiciformis* Elliott – PF; F; *291*. *Aristida stricta* Michx. var. *beyrichiana* (Trin. & Rupr.) D.B. Ward – PF, SH; C; *383a* (Ward 2001). *Arundinaria gigantea* (Walter) Walter *ex* Muhl. – RU; O; *613*. *Axonopus fissifolius* (Raddi) Kuhlm. – SH; F; *153, 349*. *Axonopus furcatus* (Flüggé) Hitchc. – RU; O; *568*. *Cenchrus echinatus* L. – RU; C; *55*. *Cenchrus incertus* M.A. Curtis – RU, SH; F; *122*. *Chasmanthium laxum* (L.) Yates var. *laxum* – SH; F; *352, 359*. *Ctenium floridanum* (Hitchc.) Hitchc. – SH; R; *J.R. Abbott 9719*. **Dactyloctenium aegyptium* (L.) Willd. *ex* Asch. and Schweinf. – RU, C, *253*. *Dichanthelium aciculare* (Desv. *ex* Poir.) Gould & C.A. Clark – SH; C; *507*. *Dichanthelium acuminatum* (Sw.) Gould & C.A. Clark var. *acuminatum* – SH; F; *209*. *Dichanthelium ensifolium* (Baldwin *ex* Elliott) Gould var. *ensifolium* – PF; R; *69*. *Dichanthelium laxiflorum* (Lam.) Gould – CS; F; *380b, 508*. *Dichanthelium ovale* (Elliott) Gould & C.A. Clark – SH; F; *1*. *Dichanthelium strigosum* (Muhl. *ex* Elliott) Freckmann var. *leucoblepharis* (Trin.) Freckmann – CS; O; *100, 297*. *Digitaria ciliaris* (Retz.) Koeler – RU; F; *292, 584*. **Echinochloa crusgalli* (L.) P. Beauv. – RU; F; *406, 585, 592*. **Eleusine indica* (L.) Gaertn. – RU; F; *168, 586*. **Eragrostis amabilis* (L.) Wight & Arn. – RU; O; *213*. *Eragrostis elliottii* S. Watson – SH; F; *261*. **Eremochloa ophiuroides* (Munro) Hack. – RU; C; *207, 295*. *Eustachys petraea* (Sw.) Desv. – RU, SH; F; *53b, 124*. *Gymnopogon ambiguus* (Michx.) Britton, Sterns & Poggenb. – SH; R;

J.R. Abbott 9722. Heteropogon melanocarpus (Elliott) Elliott *ex* Benth. – RU; O; *597.* **Lolium perenne* L. – RU; F; *546. Oplismenus hirtellus* (L.) P. Beauv. – RU; O; *642. Panicum anceps* Michx. – RU; O; *169, 182b, 324. Panicum hemitomon* Schult. – CS; C; *554.* **Panicum repens* L. – SH; F; *205. Panicum rigidulum* Bosc *ex* Nees – FD; O; *605. Panicum verrucosum* Muhl. – PF; O; *358.* **Paspalum notatum* Fluegge var. *saurae* Parodi – RU; F; *53a. Paspalum praecox* Walter – PF; R; *L. Johnson 14. Paspalum setaceum* Michx. – PF; F; *182a, 321.* **Paspalum urvillei* Steud. – RU, SH; O; *353, 521. Saccharum giganteum* (Walter) Pers. – PF; O; *374. Sacciolepis striata* (L.) Nash – CS; F; *216, 325. Schizachyrium scoparium* (Michx.) Nash var. *scoparium* – PF, SH; F; *638. Setaria corrugata* (Elliott) Schult. – PF; O; *178. Setaria parviflora* (Poir.) Kerguelen – RU; O; *138, 202. Sorghastrum secundum* (Elliott) Nash – PF, SH; C; *267.* **Sorghum halepense* (L.) Pers. – RU; F; *322, 540. Sphenopholis obtusata* (Michx.) Scribn. – RU; O; *438.* **Sporobolus indicus* (L.) R. Br. var. *indicus* – PF, RU; C; *120, 156, 348. Sporobolus juncea* (P. Beauv.) Kunth – SH; F; *506. Stenotaphrum secundatum* (Walter) Kuntze – RU; C; *323. Tridens flavus* (L.) Hitchc. – PF; O; *628. Triplasis americana* P. Beauv. – SH; R; *J.R. Abbott 9720a.* **Urochloa racemosa* (L.) Nguyen – RU; O; *583.*

POLYGALACEAE. *Polygala cymosa* Walter – FD; R; *L.J. Lehtonen 359, 450. Polygala grandiflora* Walter – PF, SH; O; *26, 82. Polygala incarnata* L. – SH; R; *587. Polygala lutea* L. – PF; R; *68. Polygala nana* (Michx.) DC. – PF; R; *184, 612. Polygala setacea* Michx. – PF; O; *179.*

POLYGONACEAE. *Eriogonum tomentosum* Michx. – SH; O; *191. Polygonella gracilis* Meisn. – SH; C; *263. Polygonum hydropiperoides* Michx. – RU; C; *411. Polygonum punctatum* Elliott – RU; R; *572. Rumex verticillatus* L. – RU; R; *433.*

PONTEDERIACEAE. *Pontederia cordata* L. – CS; R; *652.*

PORTULACACEAE. **Portulaca amilis* Speg. – RU; F; *515.*

RHAMNACEAE. *Berchemia scandens* (J. Hill) K. Koch – PF; R; *282. Ceanothus microphyllus* Michx. – SH; O; *336, 478.*

ROSACEAE. **Eriobotrya japonica* (Thunb.) Lindl. – RU; R; *640. Photinia pyrifolia* (Lam.) K.R. Robertson & J.B. Phipps – PF; O; *345. Prunus serotina* Ehrh. var. *serotina* – RU; F; *536, 571, 646. Prunus umbellata* Elliott – RU; R; *432. Rubus argutus* Link – PF; O; *338. Rubus cuneifolius* Pursh – PF, SH; C; *39.*

RUBIACEAE. *Cephalanthus occidentalis* L. – CS, FD; O; *81. Diodia teres* Walter – PF; O; *136, 175. Diodia virginiana* L. – FD; R; *542. Galium aparine* L. – RU; O; *443. Galium pilosum* Aiton – SH; O; *111. Houstonia procumbens* (J.F. Gmel.) Standl. – RU, SH; O; *430* (Wunderlin and Hansen 2003). *Mitchella repens* L. – CS, RU; O; *471.* **Oldenlandia corymbosa* L. – RU; R; *595* (Wunderlin and Hansen 2003). **Richardia brasiliensis* Gomes – RU; O; *18.* **Richardia scabra* L. – RU; R; *L.J. Lehtonen 462.*

RUTACEAE. *Zanthoxylum clava-herculis* L. – RU; R; *497.*

SALICACEAE. *Populus deltoides* W. Bartram *ex* Marshall – CS; R; *602*. *Salix caroliniana* Michx. – CS; F; *610*.

SAPINDACEAE (including Aceraceae). *Acer negundo* L. – RU; O; *524*. *Acer rubrum* L. – CS, RU; C; *296*, *460*.

SARRACENIACEAE. *Sarracenia minor* Walter – CS, PF; F; *72*.

SAURURACEAE. *Saururus cernuus* L. – CS, RU; O; *473*, *529b*.

SCROPHULARIACEAE. **Verbascum thapsus L.*—RU; O; *547*.

SMILACACEAE. *Smilax auriculata* Walter – PF, RU, SH; C; *12*, *32*, *50*. *Smilax bona-nox* L. – PF, RU; O; *372*. *Smilax glauca* Walter – PF, SH; C; *49*, *78*. *Smilax laurifolia* L. – CS; O; *308*, *449*. *Smilax smallii* Morong – PF; O; *567*. *Smilax walteri* Pursh – CS; R; *287*.

SOLANACEAE. *Physalis arenicola* Kearney – SH; R; *119*. *Solanum americanum* Mill. – RU; R; *499*.

TETRACHONDRACEAE. *Polypremum procumbens* L. – PF; O; *137*.

THEACEAE. *Gordonia lasianthus* (L.) J. Ellis – RU; O; *469*.

TURNERACEAE. *Piriqueta cistoides* (L.) Griseb. subsp. *caroliniana* (Walter) Urb. – PF, SH; F; *17* (Wunderlin and Hansen 2003).

ULMACEAE. *Ulmus alata* Michx. - RU; R; *420*.

URTICACEAE. *Boehmeria cylindrica* (L.) Sw. – RU; O; *140*, *314*. *Parietaria praetermissa* Hinton – RU; O; *440*.

VERBENACEAE. **Lantana camara* L. – RU; R; *146*. *Phyla nodiflora* (L.) Greene – RU; F; *35*, *144*. *Stylodon carneus* (Medik.) Moldenke – SH; O; *25*, *490*. **Verbena brasiliensis* Vell. – RU; O; *275*.

VIOLACEAE. *Viola lanceolata* L. – CS; O; *445*. *Viola palmata* L. – PF; O; *436*, *464*. *Viola primulifolia* L. – RU; R; *463*.

VISCACEAE (Judd et al. 2002). *Phoradendron leucarpum* (Raf.) Reveal & M.C. Johnst. – Parasite on *Quercus* sp. in CS; also parasite on *Nyssa sylvatica* var. *biflora* in FD; R; *428*, *618*.

VITACEAE. *Ampelopsis arborea* (L.) Koehne – RU; C; *565*, *596*. *Parthenocissus quinquefolia* (L.) Planch. – RU; C; *79*. *Vitis aestivalis* Michx. – RU; R; *625*. *Vitis rotundifolia* Michx. – RU; C; *47*.

XYRIDACEAE. *Xyris ambigua* Beyr. *ex* Kunth – CS; O; *234*. *Xyris brevifolia* Michx. – CS; R; *L.J. Lehtonen 439*. *Xyris caroliniana* Walter – FD, PF; F; *103*, *232*. *Xyris fimbriata* Elliott – RU; O; *581*. **Xyris jupicai* Rich. – PF; R; *J.R. Abbott 9728*. *Xyris platylepis* Chapm. – PF; R; *J.R. Abbott 9727*.

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CHROMOSOME NUMBER DETERMINATIONS IN FAM. COMPOSITAE, TRIBE ASTEREAE. VII. MOSTLY EASTERN NORTH AMERICAN AND SOME EURASIAN TAXA

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ABSTRACT. Chromosome numbers are reported for the first time for 303 individuals of 112 taxa and cultivars and five hybrids from 16 genera, nearly all from eastern Canada and the eastern United States. Counts for several taxa from China, Japan, the United Kingdom and for several garden cultivars of Old World taxa are reported. Also included are seven corrections and changes of identifications for previously published reports for taxa in *Solidago*. The majority of the reports are for asters listed in this paper under the generic name *Symphyotrichum* (including *Virgulus*) plus species of *Aster* (including *Asteromoea*, *Diplactis*, and *Kalimeris*), *Callistephus*, *Doellingeria*, *Eurybia*, *Galatella*, *Ionactis*, *Oclemena*, and *Sericocarpus*, and for goldenrods in *Solidago* and *Euthamia*. The following are first reports for the taxa: *Aster pyrenaeus* cv. "Lutetia", $2n = 36 + 2$–4 supernumeraries, cult. Ontario; *Solidago altiplanities*, $2n = 18$ from Texas; *S. arenicola*, $2n = 36$ from Alabama; *S. glomerata* $2n =$ ca. 126 ($14x$) from North Carolina; *S. speciosa* subsp. *pallida*, $2n = 18$ from South Dakota; *Symphyotrichum plumosum*, $2n = 8$ (two populations) from Florida; and *S. tradescanti*, $2n = 32$ from Maine. All other counts confirm previous reports for the taxa. A number of the reports are for rare taxa in Ontario: *Solidago arguta*, $2n = 18$, first count for Ontario; *Symphyotrichum praealtum* var. *praealtum*, $2n = 32$; *S. prenanthoides*, $2n = 32$, first counts for Ontario (8 populations); and *S. shortii*, $2n = 16$. A number of the counts are first reports for a particular taxon in a state (e.g., *Solidago altissima* subsp. *altissima*, $2n = 36$ from Tennessee; *S. brachyphylla*, $2n = 18$ from Florida; *S. canadensis* var. *hargeri*, $2n = 18$ from Virginia; *Symphyotrichum novae-angliae*, $2n = 10$ from Georgia and North Carolina; *S. priceae*, $2n = 64$ from Georgia). Differences in the karyotypes of Old and New World species of asters are discussed.

Key Words: Compositae, Astereae, chromosome numbers, *Aster*, *Chrysopsis*, *Eurybia*, *Pityopsis*, *Solidago*, *Symphyotrichum*

Determining the distribution patterns of cytotypes requires numerous counts from the range of a taxon. The determinations listed below are reported as contributions to such studies. This is the seventh in a continuing series of general reports on Astereae by the first author's

laboratory (Semple 1985; Semple and Chmielewski 1987; Semple et al. 1989, 1992, 1993, 2001).

MATERIALS AND METHODS

Meiotic counts were made from pollen mother cells (PMCs) dissected from buds fixed in the field in 3:1 EtOH : glacial acetic acid and subsequently stored under refrigeration in 70% EtOH. Mitotic counts were made from root tip cells taken from transplanted wild rootstocks or from seedlings grown from achenes collected in the wild. Root tips were pretreated in 0.01% colchicine or saturated paradichlorobenzene for 2–3 hr., fixed in either Modified Carnoy's Fixative (4:3:1 chloroform : EtOH : glacial acetic acid) or Acetic Alcohol Fixative (3:1 EtOH : glacial acetic acid) and hydrolyzed in 1N HCl for 25–30 min. at 60°C before squashing. Anther sacs containing PMCs and meristematic root tips were squashed in 1% acetic orcein, and counts of chromosomes were made from freshly prepared material. Permanent slides were made for new reports as described by Semple et al. (1981) and remain in the possession of J.C.S.

Vouchers for all counts are deposited in WAT. Identifications were made by J.C.S. In some cases, voucher specimens did not fit a published taxon description in one or more minor traits, such as amount of pubescence; these cases are indicated by the "aff." qualifier in the Appendix.

RESULTS AND DISCUSSION

Chromosome numbers are reported in the Appendix for 303 individuals of 112 taxa and cultivars and five hybrids from 16 genera nearly all from eastern Canada and the eastern United States. Included in the Appendix are reports for several taxa from China, Japan, the United Kingdom, and a half dozen garden cultivars of Old World taxa. Also included in the Appendix are seven corrections or changes of identification in *Solidago*. Wild populations were sampled in four provinces in Canada and 16 states in the United States. In total, 264 new reports are for asters and goldenrods: *Aster*, *Doellingeria*, *Eurybia*, *Galatella*, *Ionactis*, *Oclemena*, *Sericocarpus*, *Symphyotrichum* (including *Virgulus*), and *Solidago* and *Euthamia*, respectively. The following are first reports for the taxa: *Solidago altiplanities*, $2n = 9_{II}$ from Texas; *S. arenicola*, $2n = 36$ from Alabama; *S. glomerata*, $2n =$ ca. 126 from North Carolina; *S. speciosa* subsp. *pallida*, $2n = 18$ from South Dakota; *Symphyotrichum plumosum*, $2n = 8$ (two populations) from Florida; and *S. tradescanti*, $2n = 32$ from Maine. All other counts

confirm previous reports for the taxa and most are presented without comment. A number of the reports are for rare taxa in Ontario: *Solidago arguta*, $2n = 18$, first count for Ontario; *Symphyotrichum praealtum* var. *praealtum*, $2n = 32$; *S. prenanthoides*, $2n = 32$, first counts for Ontario (8 populations); and *S. shortii*, $2n = 16$. A number of the counts are first reports for a particular taxon in a state: *Solidago altissima* subsp. *altissima*, $2n = 36$ from Tennessee; *S. brachyphylla*, $2n = 18$ from Florida; *S. canadensis* var. *hargeri*, $2n = 18$ from Virginia; *Symphyotrichum novae-angliae*, $2n = 10$ from Georgia and North Carolina; and *S. priceae*, $2n = 64$ from Georgia.

The Appendix includes data corrections or changes of identification for seven previously reported counts of *Solidago*. Six note changes in identification as a result of work done in preparing the treatment of *Solidago* for the Flora North America project (Semple and Cook, in press). The seventh corrects errors in reporting the ploidy level and location data. The first report of $2n = 18$ for *S. altiplanities* was previously reported as a count for *S. speciosa* var. *angustata* (Semple and Chmielewski 1987). The report of $2n = 36$ for *S. altissima* subsp. *altissima* from a glade in Davidson Co., Tennessee was previously reported as a count for *S. canadensis* aff. var. *canadensis* (Semple et al. 1992). The first report of $2n = 18$ for *S. speciosa* subsp. *pallida* from South Dakota was previously reported as a count for *S. speciosa* var. *angustifolia* (Semple et al. 1984). Two tetraploid counts for *S. leavenworthii* from Florida were previously reported under the name *S. petiolaris* (Semple et al. 1984). The tetraploid report for *S. mollis* var. *mollis* from Oklahoma was previously published as *S. mollis* var. *angustifolia*, $2n = 9II$ (Semple and Chmielewski 1987). And lastly, the tetraploid report for *S. shortii* from Nicholas Co., Kentucky was previously published in error as $2n = 18$ from Flemming Co.: S of town of Bluelicks, S banks of Bluelicks R. (Semple et al. 1993); this confirms the previous reports for the species by Beaudry (1963).

ADDITIONAL COMMENTS ON GENERIC LIMITS OF ASTERS

In the previous paper in this series (Semple et al. 2001), a significant shift in how asters were treated was adopted over earlier papers in the series; western North American asters were placed in *Eurybia*, *Eucephalus*, *Ionactis*, *Oreostemma*, *Sericocarpus*, and *Symphyotrichum*. In this paper, eastern North American asters are treated in *Doellingeria*, *Eurybia*, *Ionactis*, *Oclemena*, *Sericocarpus*, and *Symphyotrichum*. The difference between treatments in the two papers is due strictly to the

distributions of the genera in North America. *Eucephalus* and *Oreostemma* are western North American genera, while *Doellingeria* and *Oclemena* are eastern North American. Molecular data conclusively show that *Aster* in the new restricted sense is Eurasian, with only one arctic-alpine species, *A. culminis* A. Nels., occurring in North America (Brouillet et al. 2001a, 2001b; Semple et al. 2002, unpubl. data). The genera of asters native to North America are basal or near basal members of several clades within the North American Clade of the tribe Astereae (Brouillet et al. 2001a, 2001b; Noyes and Rieseberg 1999; Semple et al. 2002, unpubl. data). Although Xiang (1994) and Xiang and Semple (1996) presented data on chloroplast DNA restriction site variation that demonstrated conclusively that the genus *Aster sensu* Jones (1980) and *sensu* Semple and Brouillet (1980) was polyphyletic, their sample did not include sufficient numbers of non-aster taxa to reveal the monophyly of the North American clade. Nesom (1994) presented a revised overview of the asters and made a large number of combinations in a number of the segregate genera that he recognized on morphological grounds. Other combinations were proposed in previous papers or subsequently (Nesom 1992, 1993a, 1993b; Semple et al. 2002; Wunderlin and Hansen 2001). Semple et al. (1996) proposed an alternative nomenclature in which many of the species Nesom placed in the genera *Canadanthus*, *Eurybia*, and *Symphyotrichum* (including *Virgulus*) were retained in *Aster*, while accepting the need to recognize *Diplactis*, *Doellingeria*, *Eucephalus*, *Ionactis*, *Oreostemma*, and *Oclemena* as separate genera. This latter scheme was rejected (Semple et al. 2002) in favor of the nomenclature adopted in here, which is very much in agreement with Nesom (1994). To facilitate the transition from the nomenclature accepted in previous papers in this series to what we believe will ultimately become the generally accepted nomenclature, the older names are given in brackets in the Appendix.

Comparison of karyotypes of Eurasian and North American asters. Included in this paper are reports for 14 taxa/cultivars and one hybrid of Eurasian asters and aster-like genera (Appendix): *Aster ageratoides* (two subspecies and one cultivar), *A. alpinus*, *A. amellus* (two cultivars, one sold as *A. pyrenaeus* cv. "Lutetia"), *A. ×frikartii* (*A. amellus* × *A. thomsonii*), *A. mongolicus A. scaber*, *A. tataricus*, *A. tongolensis*, *Callistephus chinensis*, *Galatella punctata*, and *Heteropappus hispidus*. The size of the chromosomes of all these $x = 9$ taxa were much larger than the chromosomes of any of the $x = 9$, 8, or 7 taxa of aster genera in the North American clade: *Ampelaster*, *Canadanthus*,

Eurybia, *Doellingeria*, *Ionactis*, *Oclemena*, *Sericocarpus*, and *Symphyotrichum*. Even the large chromosomes of the $x = 4$ *Symphyotrichum concolor* and *S. plumosum* were not as large as most of the chromosomes in the karyotypes of the Eurasian taxa examined. Huziwara (1959) first noted this size difference between Asiatic asters and North American asters. Based on observations made for this paper and Semple et al. (2001), it appears that in general Eurasian asters have larger chromosomes than most, if not all North American Astereae, with the possible exception of the very derived low base number taxa such as *Machaeranthera gracilis* (Nutt.) Shinners. Huziwara (1959) noted that the Japanese species of *Erigeron* he examined had small chromosomes like North American species of the genus, which is North American in origin (Noyes 2000; Noyes and Rieseberg 1999). Further study is needed on many more taxa to determine how general the trend is for non-North American Astereae to have larger chromosomes than members of the North American clade. Based on published ideograms (Grau 1973), the size range in chromosomes among species of the African genus *Felicia* is similar to that observed in this paper for Eurasian and North America species of asters. The count for *Felicia amelloides* reported here in the Appendix is a meiotic count and thus the karyotype was not analyzed. Likewise, many reported counts for Astereae are meiotic and much additional work is needed to obtain mitotic karyotype data. Furthermore, differences in techniques used in preparing mitotic counts make published information potentially inconsistent, particularly in terms of the size and degree of coiling of the chromosomes. Any comprehensive survey of Astereae chromosome size will need to take these inconsistencies into consideration.

Nesom (1994) noted that in *Aster sensu lato* the classification of NOR chromosomes ("satellite"; nucleolar organizer region bearing chromosomes) presented by Semple et al. (1983) needed review because the "euaster" type was based on species no longer included in *Aster*. Nesom (1994) referred to the "euaster" type of Semple et al. (1983) as the "eurybia" type, which has the NOR near the centromere resulting in a large distal portion (satellite) and a small proximal portion on the short arm of the NOR chromosome. This type is found in *Eurybia* and *Symphyotrichum*, and, therefore, potentially it is derived at least twice in the North American asters. Since the chromosome classification was based on a pre-molecular understanding of the asters and since it was based on North American taxa, a full review of NOR chromosomes is needed for the entire tribe. Clearly, the "primitive" NOR type of Semple et al. (1983) is at best only applicable to the North American clade,

which is the most derived group in the tribe (Brouillet et al. 2001a, 2001b; Noyes and Rieseberg 1999; Semple et al. 2002). The NOR chromosome of *Aster* in the new strict sense is illustrated well in Chatterji (1962) for that of *A. amellus* and in Tara (1972) for several eastern Asian asters. The NOR of the triploid cultivar of *Galatella punctata* (*Aster sedifolius*) observed in our study had a smaller distal satellite and a more median centromere than the *Aster* karyotypes, but the chromosomes in both were large. The NOR chromosomes of *Felicia* illustrated in Grau (1973) are similar to, though in some cases significantly larger than, the "virguloid" type of North American *Symphyotrichum* subg. *Virgulus*. Nesom (1994) referred to the Old World NOR type as the "Asterinae" type, based primarily on published karyotypes in Huziwara (1962 and cited papers) and Chatterji (1962), but without additional cytological observations. Further work is needed to see if this NOR type is shared by many non-aster Old World and South American taxa in a wide range of genera. As with karyotype size, trends in NOR chromosome morphology need to be reassessed to determine if there are any generalities to be made.

Included in this paper are counts for two species of *Doellingeria sensu* Nesom (1993b): *D. infirma* and *D. scabra* (treated here as *Aster scaber*). Nesom (1993b) placed the latter in the eastern Asian taxon *Doellingeria* sect. *Cordifolium* (Kitamura) Nesom. Our living collections of *A. scaber*, however, had involucral traits more similar to those of species of *Eucephalus* of western North America than *Doellingeria* of eastern North America (*sensu* Semple and Chmielewski, in press; synonym: *Aster* sect. *Triplopappus*, Semple et al. 1991; includes the type of genus *D. umbellata*). The chromosomes of the three species of *Doellingeria* (permanent slides in the first author's collection) were smaller than the Asiatic aster species examined, including *A. scaber*. Huziwara (1962) reported that he did not observe a big difference between his one sample of *D. umbellata* (cultivated plant from the Jardin Botanique, Montréal, Québec) and other Asiatic asters, which did not include Asiatic species of *Doellingeria sensu* Nesom. Molecular studies (Brouillet et al. 2001a, 2001b, unpubl. data) indicate the Asiatic species belong either in *Aster* in the revised sense or possibly in a new segregate genus, if the Eurasian genus *Aster* is divided up further following more detailed phylogenetic studies of the Eurasian taxa.

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APPENDIX

CHROMOSOME NUMBER DETERMINATIONS OF ASTEREAE

Chromosome number determinations of Astereae from Canada and the United States are arranged alphabetically by species. Collectors' names are abbreviated as follows: *C* = R. Cook; *C & C* = R. Cook & D. Cook; *Ch* = J. G. Chmielewski; *F* = S. Faulkenham; *S* = J. Semple; *Zh* = J. Zhang. All vouchers are deposited in WAT.

Aster ageratoides Turcz. subsp. *leiophyllus* (Franch. & Sav.) Kitam. – $2n = 36$. JAPAN. Okayama Pref.: Niimi City, Niimi, *Tara s.n.* (count from seedling).

A. ageratoides Turcz. subsp. *ovatus* (Franch. & Sav.) Kitam. – $2n = 36$. JAPAN. Okayama Pref.: Okayama City, Mt. Hauda, *Tara s.n.* (count from seedling).

A. ageratoides Turcz. variegate-leaved cultivar – $2n = 36$. CANADA. Ontario: Waterloo Reg. Mun., Waterloo, 207 Candlewood Cres., garden cultivar, *S 11013*. [sold under the name *Kalimeris incisa* (Fisch.) DC. cv. "variegata" but the cypsellae have a well-developed pappus not found in the *Kalimeris* group of asters].

Aster alpinus L. cv. "Goliath" – $2n = 18$. CANADA. Ontario: Waterloo Reg. Mun., Waterloo, 207 Candlewood Cres., cultivated in garden (source: Epic Perennials Ltd.), *S 11003*.

A. amellus L. cv. "Violet Queen" – $2n = 54$. CANADA. Ontario: Waterloo Reg. Mun., Waterloo, 207 Candlewood Cres., cultivated in garden, *S 11008* (source: Heritage Perennials Ltd.).

A. ×*frikartii* ex hort. Frikart Nursery in Switzerland (*A. amellus* L. × *A. thomsonii* C.B. Clarke) – $2n = 54$. CANADA. Ontario: Waterloo Reg. Mun., Waterloo, 207 Candlewood Cres., cultivated in garden, *S 11012* (source: Heritage Perennials Ltd.).

A. mongolicus Franch. [*Asteromoea mongolica* (Franch.) Kitam.] – $2n = 18$. CANADA. Ontario: Waterloo Reg. Mun., Waterloo, 207 Candlewood Cres., cultivated in garden, *S 11002*.

A. pyrenaeus Desf. *ex* DC. cv. "Lutetia" – $2n = 36 + 2$–4 supernumeraries.

CANADA. Ontario: Waterloo R. M., Waterloo, 207 Candlewood Cres., cultivated in garden, *S 11104*. [Semple et al. (2002) noted that this cultivar may be derived from *A. amellus* rather than *A. pyrenaeus*.]

A. scaber Thunb. – $2n = 18$. CHINA. Beijing, outskirts of city, *Li Nan s.n.* (count from seedling). JAPAN. Okayama Pref.: Niimi City, Niimi, *Tara s.n.* (count from seedling).

A. tataricus L. f. – $2n = 54$. U.S.A. North Carolina: Guilford Co., Hwy. 220 3 km N of Greensboro, escaped from cult., *Ch & Hart 393*. Virginia: Grayson Co., VA-16 0.4 km N of Troutdale (Co. Rd.-602), *S 10749*.

A. tongolensis Franch. – $2n = 54$. CANADA. Ontario: Waterloo Reg. Mun., Waterloo, 207 Candlewood Cres., cultivated in garden, *S 11004*.

Boltonia diffusa Elliott – $2n = 18$. U.S.A. Florida: Franklin Co., S of Sumatra, Apalachicola N.F., junction of For. Rd.-129 and For. Rd.-129A, *S 10926*.

Callistephus chinensis (L.) Nees – $2n = 18$. CANADA. Ontario: Waterloo Reg. Mun., Waterloo, 207 Candlewood Cres., garden cultivar, *S 11011*.

Chrysopsis floridana Small – $2n = 5_{II}$. U.S.A. Florida: Hillsborough Co., Apollo Beach, I-75 S entrance ramp right-of-way off FL-672, *S, Wunderlin & Walker 10889*; Riverview, Stirling Downs ELLAPPA, near Boyette Rd. and McMullen Rd., *S, Wunderlin & Walker 10885*.

C. godfreyi Semple f. *godfreyi*. – $2n = 5_{II}$. U.S.A. Florida: Escambia Co., Pensacola Beach, E end of town, FL-399, lot between elementary school and church, *S 10944*; Gulf Co., SE of Port St. Joe, US-98 2.8 km SE of Co. Rd.-C30A, *S 10922*.

C. gossypina (Michx.) Nutt. subsp. *cruiseana* (Dress) Semple – $2n = 9_{II}$. U.S.A. Florida: Okaloosa Co., Destin, dune remnant between Co. Rd.-2378 (old US-98) and US-98, SE of Best Western Motel and N of Scampi's, *S 10942*. – $2n = 18$. Florida: Walton Co., Dune Allen, Co. Rd.-30A W of Grayton Beach, *S 10565*.

C. gossypina (Michx.) Nutt. subsp. *gossypina* f. *gossypina* – $2n = 9_{II}$. U.S.A. Florida: Leon Co., SE of Tallahassee, US-319 ca. 4.5 km S of US-27, *S 10553*; Levy Co., NW of Chiefland, US-98 1.6 km SW of Co. Rd.-218, SW of Fanning Springs, *S 10913*.

C. lanuginosa Small – $2n = 5_{II}$. U.S.A. Florida: Bay Co., Panama City Beach, US-98 3.2 km W of US-98alt. (E), *S 10936*.

C. lanuginosa × *C. linearifolia* subsp. *linearifolia* – $2n = 5_{II}$, some irregularities. U.S.A. Florida: Bay Co., Panama City Beach, US-98 0.9 km E of FL-79, highly disturbed vacant lot by Escanaba Ave., *S 10939*. [Meiosis was regular in most PMCs; some cells have one multivalent; anaphase I and II appears normal with no bridges or lagging fragments; no micro pollen grains were observed in near-mature anthers.]

C. linearifolia Semple subsp. *linearifolia* – $2n = 5_{II}$. U.S.A. Florida: Bay Co., Panama City Beach, US-98 0.9 km E of FL-79, highly disturbed vacant lot by Escanaba Ave., *S 10937*.

C. mariana (L.) Elliott – $2n = 8_{II}$. U.S.A. Florida: Marion Co., NW of Ocala, US-27 0.6 km SE of Blichton (Co. Rd.-326), *S 10910*. – $2n = 24$. Georgia: Dade Co., SE of Trenton, Lookout Mt., GA-136 0.4 km E of Sunset Rd., W of Cloudland Canyon St. Pk., *S 10990* (seedling). – $2n = 32$. Florida: Marion Co., W of Citra, Co. Rd.-318 1.6 km W of US-301, *S 10963*.

C. scabrella Torr. & A. Gray – $2n = 5_{II}$. U.S.A. Florida: Hillsborough Co., Tampa, University of South Florida, USF Biological Reserve, *S, Wunderlin & Walker 10890*; Marion Co., N of Lake Bryant, FL-40 at SE 165 Ave., E of Waldena, *S*

10909. – $2n = 10$. Florida: Lake Co., FL-19 9.5 km N of Altoona (FL-42), *S 10906* (seedling); Marion Co., S of Citra, US-231 3.1 km SW of Co. Rd.-318, *S 10964* (seedling).

C. aff. *scabrella* Torr. & A. Gray – $2n = 5_{II}$. U.S.A. Florida: Charlotte Co., NE of Cleveland, S of Shell Creek, Co. Rd.-764 E of FL-17, *S, Wunderlin, Walker, Delaney & Cochrane 10901* (plants have a more open lax capitulescence than typical *C. scabrella*).

Doellingeria infirma (Michx.) E.L. Greene – $2n = 18 + 2$ supernumeraries. U.S.A. West Virginia: Pocahontas Co., NW of Mill Point, Monongahela Nat'l. For., near junction of For. Rd.-102 and For. Rd.-107, *S 10716*.

Erigeron vernus (L.) Torr. & A. Gray – $2n = 18$. U.S.A. Georgia: Clinch Co., E of Fargo, GA-177 3.4 km NE of US-441, *S 10884*.

Eurybia avita (Alexander) G.L. Nesom [*Aster avitus* Alexander] – $2n = 36$. U.S.A. Georgia: Rabun Co., N of Tallulah Falls, US-441 2 km N of county line, *S 10861*.

E. chlorolepis (E.S. Burgess *in* Small) G.L. Nesom [*Aster chlorolepis* E.S. Burgess *in* Small] – $2n = 36$. U.S.A. Virginia: Grayson Co., Jefferson Nat'l. For., along Cabin Creek near hairpin turn on US-58, W of For. Rd.-797, *S 10757*.

E. compacta G.L. Nesom [*Aster gracilis* Nutt.] – $2n = 18$. U.S.A. New Jersey: Burlington Co., NE of Chatsworth, junct. of Co. Rd.-532 and NJ-72, *S 10370*; Ocean Co., W of Barnegat, Co. Rd.-554 1.7 km E of NJ-72, *S 10371*.

E. divaricata (L.) G.L. Nesom [*Aster divaricatus* L.] – $2n = 18$. U.S.A. Kentucky: Pike Co., SE of Canada, old US-119 3.1 km NW of KY-199 and Huddy, *S 10779*. North Carolina: Henderson Co., W of Avery Creek, Pisgah Nat'l. For., For. Rd.-479 1.6 km SW of NC-2, *S 10833*; Watauga Co., E of village of Beech Creek, US-321 0.7 km E of McGuire Rd., *S 10792*. Pennsylvania: Greene Co., PA-18 4 km SW of Holbrook, junction of Tom's Run Rd., *S 10674*; Lawrence Co., McConneth Mill St. Pk., *C & C 50*. Virginia: Bath Co., W of Mountain Grove, VA-39 3.1 km E of WV-92, *S 10723*. West Virginia: Greenbrier Co., Monongahela Nat'l. For., WV-39/55 by N Fork Cherry Creek, North Bend Picnic Area, *S 10710*; Marion Co., US-250 3.2 km S of Mannington, MP-19, *S 10690*; Nicholas Co., S of Birch River, Youngs Monument Rd. 0.6 km NW of US-19, along Brown's Ridge, *S 10696*.

E. surculosa (Michx.) G.L. Nesom [*Aster surculosus* Michx.] – $2n = 36$. U.S.A. North Carolina: Cherokee Co., US-64 7.8 km W of Ranger, *S & J.W. Semple 10351*.

Euthamia caroliniana (L.) E.L. Greene – $2n = 18$. U.S.A. Georgia: Echols Co., W of Statenville, GA-376, flood plain of Little R., *S 10877*.

E. graminifolia (L.) Nutt. – $2n = 18$. CANADA. Ontario: Waterloo Reg. Mun., Waterloo, University of Waterloo, along Laurel between Biology 2 and Minota Hagey Residence, *C & S 7*. U.S.A. Pennsylvania: Forest Co., Hwy-62 N of E Hickory, *C & C 63*.

Felicia amelloides (L.) Voss cv. "variegated" – $2n = 9_{II}$. CANADA. Ontario: Waterloo Reg. Mun., Waterloo, 207 Candlewood Cres., garden cultivar, *S 11009*.

Galatella punctata (Waldst. & Kit.) Nees [*Aster sedifolius* L. subsp. *sedifolius* cv. *nanus*; *A. canus* Waldst. & Kit. subsp. *punctatus* (Waldst. & Kit.) Soö] – $2n = 27$ (triploid). CANADA. Ontario: Waterloo Reg. Mun., Waterloo, 207 Candlewood Cres., garden cultivar, *S 11014*.

Heteropappus hispidus (Thunb.) Less. – $2n = 36$. CHINA. Beijing, *Li Nan s.n.* (count from seedling).

Ionactis linariifolia (L.) E.L. Greene [*Aster linariifolius* L.] – $2n = 9_{II}$. U.S.A.

Georgia: Taylor Co., E of Butler, GA-96 4.7 km E of GA-137, *S 10969*. – $2n = 18$. Virginia: Allegheny Co., US-220 6.7 N of Covington, S of scenic view area, *S 10731*.

Oclemena acuminata (Michx.) E.L. Greene – $2n = 18$. CANADA. Ontario: Haliburton Co., along road to W side of Paudash Lake, near boat launch, *S 10666*. U.S.A. North Carolina: Mitchell Co., Roan Mt., Garden Trail, W of parking lot near information booth, *S 10808*. Virginia: Grayson Co., Grayson Highlands St. Pk., Wilson Creek Trail along Wilson Creek, *S 10754*; Wythe Co., SW of Speedwell, Iron Mt., N side of Comers Rock, For. Rd.-57 5.5 km W of US-21, *S 10782*.

Pityopsis aspera (Shuttlew. *ex* Small) Small var. *adenolepis* (Fernald) Semple & F.D. Bowers - $2n = 18_{II}$. U.S.A. Florida: Okaloosa Co., E of Destin, Crystal Beach Drive, *S 10562*; also $2n = 36$ (from rootstock).

P. graminifolia (Michx.) Nutt. var. *aequilifolia* F.D. Bowers & Semple – $2n = 9_{II}$. U.S.A. Florida: Marion Co., FL-40 9.6 km W of Juniper Springs, Ocala Nat'l. For., 1.0 km E of For. Rd.-579, *S 10908*; Polk Co., N of Withla, Co. Rd.-33 1.0 km S of Lake Co. line, *S 10905*.

P. graminifolia (Michx.) Nutt. var. *latifolia* (Fernald) Semple & F.D. Bowers – $2n = 18_{II}$. U.S.A. Florida: Polk Co., SW of Withla, Deen Still Rd. 2.1 km W of Co. Rd.-33, *S 10904*. - $2n = 36$. Virginia: Southhampton Co., US-258 2.3 mi. N of Nottaway R., *S & Ch 5999*.

P. graminifolia (Michx.) Nutt. var. *tenuifolia* (Torr.) Semple & F.D. Bowers – $2n = 18$. U.S.A. Louisiana: Winn Parish, US-84 7.6 mi. W of Winnfield, junction of US-167, *S & Ch 6422*.

P. pinifolia (Elliott) Nutt. $2n = 18$. U.S.A. North Carolina: Harnett Co., NC-27 just NE of Pineview, *S 10537*.

Sericocarpus asteroides (L.) Nees [*Aster paternus* Cronquist] – $2n = 18$. U.S.A. Georgia: Dade Co., SE of Trenton, upper el. Lookout Mt., GA-136 0.4 km E of Sunset Rd., W of Cloudland Canyon St. Pk., *S 10991*.

S. tortifolius (Michx.) Nees [*Aster tortifolius* Michx.] – $2n = 18$. U.S.A. Florida: Franklin Co., S of Sumatra, Ft. Gadsden Historical Site, junction of For. Rd.-129 and For. Rd.-129C, *S 10923*; Hamilton Co., W of Jasper, junction of US-41 and FL-6, *S 10966*.

Solidago altiplanities C.E.S. Taylor & R.J. Taylor – $2n = 9_{II}$. U.S.A. Texas: Cottle Co., US-82 N of Paducah, 2.7 km S of North Pease R., *S 8234* [previously published as *S. speciosa* Nutt. var. *rigidiuscula* (Semple and Chmielewski 1987) and corrected here].

S. altissima L. subsp. *altissima* – $2n = 36$. U.S.A. Tennessee: Davidson Co., junction of TN-171 and US-41, *S & Ch 9124* [previously published as *S. canadensis* aff. var. *canadensis* (Semple et al. 1992) and corrected here]. – $2n = 54$. CANADA. Ontario: Essex Co., Maidstone Twp., Hwy.-22 W of Puce, Wallace Woods, *C & Parks 21*; Grey Co., Co. Rd.-12 W of Markdale, E of ON-6, *C & F 19*. U.S.A. Florida: Jackson Co., Co. Rd.-276 3.6 km N of US-231 in Alford, *S 10949*. Georgia: Dade Co., Trenton, along branch of Lookout Creek, near high school and GA-138, *S 11002*; Greene Co., N of Greensboro, Oconee N.F. boundary, GA-15, *S 10870*; Putnam Co., SW of Warfield, US-129 SW of Little R., 6.3 km W of GA-212, *S 10872*. Pennsylvania: Butler Co., Moraine St. Pk., *C & C 46*. West Virginia: Marion Co., S of Ida May, WV-216 3.8 km S of US-250, *S 10693*.

S. arenicola B.R. Keener & Kral – $2n = 36$. U.S.A. Alabama: Blount Co., NW of Cleveland, woods near Locust Creek of Warrior R., 200–300 m W of bridge on US-231, *S & B. Semple 11191*.

S. arguta Aiton var. *arguta* – $2n = 18$. CANADA. Ontario: Wellington Co., E of Guelph, Rockwoods Cons. Area, *S & Horsburgh 10574*. U.S.A. Virginia: Bath Co., W of Mountain Grove, VA-39 3.1 km E of WV-92, *S 10727*.

S. arguta Aiton subsp. *caroliniana* (A. Gray) G. Morton – $2n = 18$. U.S.A. Florida: Washington Co., S of Chipley, Falling Waters St. Rec. Area, *S 10950*. Georgia: Dade Co., SE of Trenton, NW side of Lookout Mt., GA-138 at upper hairpin turn, *S 10995*; Harris Co., E of Pine Mountain, Kings Gap Rd. 3.0 km E of GA-354, *S 10978*; S of Pine Mountain, Gallaway Gardens, *S 10981*. North Carolina: Henderson Co., W of Avery Creek, Pisgah Nat'l. For., For. Rd.-479 0.1 km S of NC-2, *S 10826*; Macon Co., S of Highlands, NC-28 8.3 km S of US-64, 0.8 km N of Wilson Rd., *S 10857*. Virginia: Grayson Co., VA-16 just S of county line, Hurricane Mt., *S 10743*; Washington Co., E of Damascus, US-58 7.1 km E of VA-91, Jefferson Nat'l. For., *S 10763*. – $2n = 36$. U.S.A. North Carolina: Transylvania Co., NC-281 near E side of Whitewater R., *S 10845*.

S. bicolor L. – $2n = 18$. CANADA. Ontario: Leeds Co., W of Rockport, woods just E of bridge to U.S.A., *S 10656*. U.S.A. North Carolina: Henderson Co., W of Avery Creek, Pisgah Nat'l. For., For. Rd.-479 0.1 km S of NC-2, *S 10827*. Pennsylvania: Greene Co., PA-18 4 km SW of Holbrook, junction of Tom's Run Rd., *S 10676*. Virginia: Allegheny Co., US-220 6.7 km N of Covington, S of Scenic View area, *S 10732*; Grayson Co., VA-16 just S of county line, Hurricane Mt., *S 10744*. West Virginia: Marion Co., US-250 2 km S of Metz, *S 10681*.

S. brachyphylla Chapm. – $2n = 18$. U.S.A. Florida: Gadsden Co., I-10 eastbound rest area, just E of Apalachicola R., *S 10957*.

S. caesia L. var. *caesia* – $2n = 18 + 1$ supernumerary. CANADA. Ontario: Elgin Co., S of Wallacetown, S of Tyrconnell, slope above small ceek near Lake Erie, *S & Zh 10583*.

S. canadensis L. var. *canadensis* – $2n = 18$. CANADA. Ontario: Bruce Co., S of Chelsey, Co. Rd.-19 1 km S of Side Rd. 30N, *C & F 14*; Hwy.-9 1.5 km SE of Carrick Twp. Rd. 30, S of Mildmay, *C & F 11*; Frontenac Co., W of Silver Lake, Hwy.-7 1.1 km E of Fall River Rd., *S 10658*; Peel Co., SE of Belfountain, by Bruce Trail, top of Niagara Escarpmant, N of Calledon Mt. Dr., *S & C 10653*. UNITED KINGDOM. SW of London, Surrey, Rochampton, Rochampton Rd., entrance way garden of Rochampton Club, *S 10390*.

S. canadensis L. var. *hargeri* Fernald – $2n = 18$. U.S.A. Virginia: Bath Co., VA-39 S of Mountain Grove, *S 10728*.

S. canadensis L. (naturalized European race) – $2n = 18$. UNITED KINGDOM. SW of London, Surrey, Barnes Rock Lane, NE of Upper Richmond Rd., S of BR-Barnes Station, *S 10389*.

S. erecta Pursh – $2n = 18$. U.S.A. Georgia: Dade Co., SE of Trenton, Lookout Mt., upper elevation, GA-136 0.4 km E of Sunset Rd., W of Cloudland Canyon St. Pk., *S 10996*; Greene Co., Oconee Nat'l. For., For. Rd. just E of GA-15 2.6 km S of Oconee R., *S 10868*; Taylor Co., SE of Carsonville, old US-19 N of GA-208, 0.6 km S of Little Patsiliga Creek, *S 10974*. Tennessee: Sullivan Co., US-421 5.8 km W of county line, *S 10771*. Virginia: Bath Co., W of Mountain Grove, VA-39 3.1 km E of WV-92, *S 10721*.

S. fistulosa Mill. – $2n = 18$. U.S.A. Florida: Washington Co., S of Chipley, Co. Rd.-77A 0.5 km S of Co. Rd.-C280, *S 10952*. Georgia: Echols Co., GA 94 2.8 3.0 km E of Statenville, *S 10879*.

S. gigantea Aiton – $2n = 18$. U.S.A. North Carolina: Transylvania Co., just NE of Conestee, US-276 8 km S of US-64 (in Brevard), *S 10842*. – $2n = 36$. CANADA. Ontario: Waterloo Reg. Mun., Waterloo, University of Waterloo, along Laurel Creek between Biology 2 and Minota Hagey Residence, *C & S 4, C & S 8*. U.S.A. North Carolina: Watauga Co., E of village of Beech Creek, US-321 0.7 km E of McGuire Rd., *S 10798*.

S. glomerata Michx. – $2n =$ ca. 126. U.S.A. North Carolina: Avery Co., Grandfather Mt., near bridge view parking lot, *S 10789*.

S. hispida Muhl. var. *hispida* – $2n = 18$. CANADA. Ontario: Bruce Co., S of South Sauble Beach, Co. Rd.-13 0.9 km S of French Bay Rd., *S 10671*; Lambton Co., Pinery Prov. Pk., Bittersweet Trail by Ausable R., *C & C 74*.

S. hispida Muhl. var. *huronensis* Semple – $2n = 18$. CANADA. Ontario: Bruce Co., Sauble Beach, dunes, *S 10672*; Lambton Co., Pinery Prov. Pk., Bittersweet Trail by Ausable R., *C & C 73*.

S. juncea Aiton – $2n = 18$. CANADA. New Brunswick: Charlotte Co., Grand Manan Is., Southwest Head area, *Hinds s.n.* Ontario: Lambton Co., Pinery Prov. Pk., Bittersweet Trail by Ausable R., *C & C 72*. U.S.A. Pennsylvania: Greene Co., PA-18 4 km SW of Holbrook, junction of Tom's Run Rd., *S 10677*. West Virginia: Marion Co., US-250 2 km SE of Metz, *S 10685*.

S. leavenworthii Torr. & A. Gray – $2n = 36$. U.S.A. Florida: Indian River Co., E of Fellsmere, *Semple et al. 7524* [previously published as *S. petiolaris* (Semple et al. 1984) and corrected here]; Taylor Co., N of Econfina, US-98 0.9 km E of Econfina R., *S 10918;* W of Hampton Springs, *Semple et al. 7443* [previously published as *S. petiolaris* (Semple et al. 1984) and corrected here].

S. mollis Bartl. var. *mollis* – $2n = 18_{II}$. U.S.A. Oklahoma: Greer Co., OK-9 E of Reed, *S & Heard 8235* [previously published as *S. mollis* var. *angustifolia* $2n = 9_{II}$ (Semple & Chmielewski 1987) and corrected here].

S. nemoralis Aiton subsp. *nemoralis* – $2n = 18$. CANADA. Ontario: Bruce Co., Co. Rd.-22 1.5 km W of Co. Rd.-10, *C & F 12*; Grey Co., junction of Hwy.-26 and Co. Rd.-112, *C & F 18*; Lambton Co., Pinery Prov. Pk., Carolinian Trail parking area, *C & C 75*; Wellington Co., E of Eramosa, Co. Rd.-124 (formerly Hwy.-24) 2.2 km W of Eramosa 5th line, *S & C 10649*. U.S.A. Ohio: Morrow Co., Mt. Gilead St. Pk., *C & C 28*; Tuscarawas Co., E of New Philadelphia, near junction of Hwy.-39 and Hendersoon School Rd., *C & C 45*. Virginia: Bland Co., S of Bastian, Appalachian Trail, just E of I-77, *S 10737*. West Virginia: Marion Co., US-250 2 km SE of Metz, *S 10682*; Nicholas Co., S of Birch River, Youngs Monument Rd. 0.6 km NW of US-19, along Brown's Ridge, *S 10704*. – $2n = 36$. CANADA. Ontario: Frontenac Co., Hwy.-7 W of Silver Lake, 1.1 km E of Fall River Rd., *S 10657*. U.S.A. Ohio: Holmes Co., E of Nashville, Hwy.-60/39 near Hwy.-754, *C & C 41*.

S. odora Aiton subsp. *chapmanii* (A. Gray) Semple – $2n = 18$. U.S.A. Florida: Hillsborough Co., Apollo Beach, I-75 S entrance ramp right-of-way off FL-672, *S, Wunderlin & Walker 10888*.

S. odora Aiton subsp. *odora* – $2n = 18$. U.S.A. Georgia: Echols Co., GA-94 2.8–3.0

km E of Statenville, *S 10878*. Florida: Jackson Co., FL-2 5.6 km E of US-231 in Campbellton, *S 10954*.

S. ohioensis Riddell – $2n = 18$. CANADA. Ontario: Bruce Co., S of South Sauble Beach, Pashwood Dr. just E of Co. Rd.-13, *S 10668*.

S. patula Muhl. subsp. *patula* – $2n = 18$. CANADA. Ontario: Elgin Co., S of Orwell, N of Springwater Cons. Area, *S & Zh 10589*; Haldimand-Norfolk Reg. Mun., Backus Woods, Conc. IV Rd., *S & Horsburgh 10575*.

S. petiolaris Aiton – $2n = 18$. U.S.A. Florida: Washington Co., S of Chipley, Falling Waters St. Rec. Area, *S 10948*.

S. puberula Nutt. subsp. *puberula* – $2n = 18$. U.S.A. North Carolina: Mitchell Co., NC-261 2.1 km below Carver Pass, *S 10815*. Tennessee: Carter Co., TN-143, Carver's Gap, just W of state line, *S 10807*.

S. rigida L. subsp. *rigida* – $2n = 36$. CANADA. Ontario: Walpole Is., NE corner, side road W of Chief Rd., *S & Zh 10603*.

S. rugosa Mill. var. *aspera* (Aiton) Fernald – $2n = 36$. U.S.A. North Carolina: Henderson Co., W of Avery Creek, Pisgah Nat'l. For., For. Rd.-479 2.8 km SW by road of NC-2, *S 10834*; Transylvania Co., just NE of Conestee, US-276 8.0 km S of US-64, *S 10843*.

S. rugosa Mill. var. *rugosa* – $2n = 18$. CANADA. Ontario: Bruce Co., between Mildmay and Harriston, Hwy.-9 1.5 km SE of Carrick Twp Rd.-30, *C & F 9*, *C & F 10*; Grey Co., Co. Rd.-25 W of Dornoch, *C & F 16*, side rd., *C & F 15*; Frontenac Co., Co. Rd.-509 NW of Robertsville Rd., *S 10664*; Wellington Co., 6th Line Rd. 0.2 km S of Co. Rd.-124, *S & C 10650*. U.S.A. Pennsylvania: Butler Co., Moraine St. Pk., Hwy.-528 ca. 2 km N of entrance, *C & C 55*. Virginia: Bland Co., S of Bastian, Appalachian Trail just E of I-77, *S 10735*. West Virginia: Marion Co., US-250 3.2 km S of Mannington, MP-19, *S 10687*. – $2n = 36$. U.S.A. Ohio: Ashland Co., Mohican St. Pk., *C & C 36*. West Virginia: Nicholas Co., S of Birch River, Youngs Monument Rd. 0.6 km NW of US-19, along Brown's Ridge, *S 10703*.

S. sempervirens L. subsp. *mexicana* (L.) Semple – $2n = 18$. U.S.A. Florida: Franklin Co., E of Apalachicola, along John Gorrie Mem. Bridge causeway, *S 10931*.

S. shortii Torr. & A. Gray – $2n = 36$. U.S.A. Kentucky: Nicholas Co., S of town of Blue Lick Springs, S banks of Licking R., *S & Suripto 9598* [previously published in error as $2n = 18$, Flemming Co.: S of town of Bluelicks, S banks of Bluelicks R. (Semple et al. 1993) and corrected here].

S. speciosa Nutt. subsp. *pallida* (Porter) Semple – $2n = 18$. U.S.A. South Dakota: Custer Co., S of Keystone, *S & Brouillet 4476* [previously published as *S. speciosa* var. *angustifolia* Torr. & A. Gray (Semple et al. 1984) and corrected here].

S. spithamaea M.A. Curtis *ex* A. Gray – $2n = 54$. U.S.A. North Carolina: Avery Co., top of Grandfather Mt., near parking lot, *S 10790*.

S. squarrosa Muhl. – $2n = 18$. CANADA. Ontario: Frontenac Co., Co. Rd.-509 NW of Robertsville Rd., *S 10663*; Haliburton Co., W of Carnarvon, Hwy.-118 2.8 km E of Anson Creek, *S 10667*.

S. stricta Aiton subsp. *stricta* – $2n = 18$. U.S.A. Florida: Dixie Co., W of Newport, US-98 0.9 km W of Co. Rd.-59, *S 10919*. – $2n = 54$. U.S.A. Florida: Dixie Co., US-98 NW of Co. Rd.-358, 6.3 km S of Tennille (FL-51), *S 10915*; Taylor Co., N of Econfina, US-98 0.9 km E of Econfina R., *S 10917*. Georgia: Echols Co., GA-94 2.8–3.0 km E of Statenville, *S 10880*.

S. tortifolia Elliott – $2n = 18$. U.S.A. Florida: Marion Co.: NW of Ocala, US-27 0.6 km SE of Blichton (Co. Rd.-326), *S 10911*.

S. uliginosa Nutt. – $2n = 18$. CANADA. Ontario: Frontenac Co., Co. Rd.-509 3.0 km N of Mississippi R., N of Snow Rd. Station, *S 10664*.

S. virgaurea L. subsp. *virgaurea* – $2n = 18$. SWEDEN. Värmland: Säldebråten (municipality of Kil), *P. Olsen s.n.*

Symphyotrichum ×amethystinum (Nutt.) G.L. Nesom [*Aster ×amethystinus* Nutt.] $2n = 10$. CANADA. Ontario: Lambton Co., N of Camlachie, Lakeshore Rd. 7.2 km NE of Co. Rd.-26, *S & Zh 10596*.

S. chapmanii (Torr. & A. Gray) Semple & Brouillet [*Aster chapmanii* Torr. & A. Gray; *Eurybia chapmanii* (Torr. & A. Gray) G.L. Nesom] – $2n = 14$. U.S.A. Florida: Franklin Co., S of Sumatra, Apalachicola Nat'l. For., For. Rd.-1290 ca. 0.5 km S of For. Rd.-129, *S 10924*; Walton Co., E of Bruce, *S & Ch 6342*.

S. concolor (L.) G.L. Nesom [*Aster concolor* L.] – $2n = 8$. U.S.A. Florida: Columbia Co., NW of Highland Springs, US-27 0.8 km NE of Santa Fe R. and Co. line, *S 10960*; Gulf Co., SE of Port St. Joe, US-98 2.8 km SE of Co. Rd.-C30A, *S 10933*; Jackson Co., FL-271 S of Co. Rd.-164, 3.4 km N of Oak Grove Rd., *S 10955*. Georgia: Dade Co., SE of Trenton, upper elevation Lookout Mt., GA-136 0.4 km E of Sunset Rd., W of Cloudland Canyon St. Pk., *S 10992*; Taylor Co., E of Butler, GA-96 4.7 km E of GA-137, *S 10970*; Walker Co., Chattahoochee Nat'l. For., Maddox Gap, GA-136 at For.Rd.-250, *S 10983*.

S. cordifolium (L.) G.L. Nesom [*Aster cordifolius* L.] – $2n = 16$. U.S.A. Kentucky: Pike Co., SE of Canada, old US-119 3.1 km NW of KY 199 and Huddy, *S 10775*. North Carolina: Watauga Co., E of village of Beech Creek, US-321 0.7 km E of McGuire Rd., *S 10793*. Virginia: Bland Co., S of Bastian, Appalachian Trail just E of I-77, *S 10740*; Washington Co., S of village of Konnarock, US-58 6.1 km NW by rd. of county line, *S 10761*. West Virginia: Pocahontas Co., Watoga St. Pk., Co. Rd.-21, *S 10717*. $2n = 32$. CANADA. Ontario: Frontenac Co., Co. Rd.-509 S of Clarendon Station, N of Burke Settlement Rd., *S 10659*. U.S.A. Georgia: Walker Co., W of LaFayette, E of Estella, GA-193 NW side of Pigeon Mt. at hairpin turn, *S 10987*. North Carolina: Macon Co., Highlands, NC-28 0.6 km S of US-64, opposite U.S. Post Office, *S 10855*. Ohio: Morrow Co., Mt. Gilead St. Pk., *C & C 29*. Pennsylvania: Greene Co., PA-18 0.8 km S of Nettle Hill, *S 10678*; Venango Co., PA-208 mp50, *C & C 57*. South Carolina: Greenville Co., US-276 5.2 km S (by rd.) of entrance to Caesar's Head St. Pk., *S 10840*. Virginia: Bath Co., W of Mountain Grove, VA-39 3.1 km E of WV-92, *S 10725*. West Virginia: Nicholas Co., S of Birch River, Youngs Monument Rd. 0.6 km NW of US-19, along Brown's Ridge, *S 10699*.

S. dumosum (L.) G.L. Nesom [*Aster dumosus* L.] – $2n = 16$. U.S.A. Florida: Washington Co., S of Chipley, Co. Rd.-77A 0.5 km S of Co. Rd.-C280, *S 10951*. – $2n = 32$. U.S.A. Georgia: Dade Co., SE of Trenton, upper el. Lookout Mt., GA-136 0.4 km E of Sunset Rd., W of Cloudland Canyon St. Pk., *S 10994*; Harris Co., E of Pine Mountain, N side of Pine Mt., GA-354 W of F.D.R. St. Pk., *S 10980*.

S. elliottii (Torr. & A. Gray) G.L. Nesom [*Aster elliottii* Torr. & A. Gray] – $2n = 16$. U.S.A. North Carolina: Onslow Co., NC-50 13.1 km S of NC-53, S of Maple Hill, *S 10538*.

S. ericoides (L.) G.L. Nesom var. *ericoides* [*Aster ericoides* L. var. *ericoides*] – $2n = 10$. CANADA. Manitoba: S of Winnipeg, MB-75 1 km N of Hwy.-305, NW of

Ste. Agathe, *S 10647*. Ontario: Bruce Co., Co. Rd.-22 1.5 km W of Co. Rd.-10, *C & F 13*.

S. georgianum (Alexander *ex* Small) G.L. Nesom [*Aster georgianus* Alexander *ex* Small] – $2n = 50$. U.S.A. Georgia: Jones Co., NE of Gray, US-129 just S of Fortyville Rd., 5.5 km NE of GA-16/22, *S 10875*.

S. laeve (L.) A. Löve & D. Löve × *S. lanceolatum* (Willd.) G.L. Nesom var. *lanceolatum* – $2n = 48$. CANADA. Ontario: Lambton Co., E of Bright's Cove, Co. Rd.-7 at Lambert Rd., *S & Zh 10600*.

S. lanceolatum (Willd.) G.L. Nesom var. *hirsuticaule* (Semple & Chmiel.) G.L. Nesom – $2n = 32$. CANADA. Ontario: Waterloo Reg. Mun., Waterloo, University of Waterloo, along Laurel Creek between Biology 2 and Minota Hagey Residence, *C & S 5*; York Co., N of Ballantrae, *S, Toplack & Stranak 2084b*.

S. lanceolatum (Willd.) G.L. Nesom var. aff. *hirsuticaule* (Semple & Chmiel) G.L. Nesom – $2n = 32$. CANADA. Ontario: Kenora Dist., Hwy.-17 W of Borups Corners, floating bog mat, *S & B. Semple 6732*.

S. lanceolatum (Willd.) G.L. Nesom var. *lanceolatum* – $2n = 48$. U.S.A. Minnesota. Wilkins Co., W of Nashua, jct. MN-9 and MN-55, *S & Ch 5108*.

S. lanceolatum (Willd.) G.L. Nesom var. *latifolium* (Semple & Chmiel.) G.L. Nesom – $2n = 64$. U.S.A. Georgia: Dade Co., SE of Trenton, NW side of Lookout Mt., GA-138 at upper hairpin turn, *S 10998;* Walker Co., W of LaFayette and E of Estella, NW side of Pigeon Mt., GA-193 at hairpin turn, *S 10985*. North Carolina: Watauga Co., E of village of Beech Creek, US-321 0.7 km E of McGuire Rd., *S 10795*. Tennessee: Sullivan Co., Holston Mt., Appalachian Trail near US-421, *S 10773*. West Virginia: Braxton Co., WV-5 ca. 5 km W of Burnville (I-79), embankment of Little Kanawha R., *S 10694*; Marion Co., US-250 2 km SE of Metz, *S 10684*; Nicholas Co., S of Birch River, Youngs Monument Rd. 0.6 km NW of US-19, along Brown's Ridge, *S 10697*; WV-39 about half way between Canvas and Nettie, *S 10705*.

S. lateriflorum (L.) A. Löve & D. Löve var. *angustifolium* (Wiegand) G.L. Nesom [*Aster lateriflorus* (L.) Britton var. *angustifolius* Wiegand] - $2n = 32$. U.S.A. West Virginia: Marion Co., US-250 3.2 km S of Mannington, MP-19, *S 10691*.

S. lateriflorum (L.) A. Löve & D. Löve var. *lateriflorum* [*Aster lateriflorus* (L.) Britton var. *lateriflorus*] - $2n = 16$. CANADA. Ontario: Peterborough Co., Peterborough, *S 2064*. Québec: Garthby, Lac Aylmer, *S & Keir 4604*. U.S.A. North Carolina: Henderson Co., W of Avery Creek, Pisgah Nat'l. For., For. Rd.-479 0.1 km S of NC-2, *S 10823*. Tennessee: Unicoi Co., S of village of Flag Pond, TN-81N of Sam's Gap (NC border), *S 10819*. Virginia: Bath Co., W of Mountain Grove, VA-39 3.1 km E of WV-92, *S 10724*; Washington Co., S of village of Konnarock, US-58 6.1 km NW by rd. of county line, *S 10762*; E of Damascus, US-58 7.1 km E of VA-91, *S 10766*. – $2n = 32$. U.S.A. Florida: Washington Co., S of Chipley, Falling Waters St. Rec. Area, *S 10947*. Georgia: Greene Co., Oconee Nat'l. For., GA-15 by Harris Creek, 4.5 km S of Oconee R., *S 10869*; Harris Co., E of Pine Mountain, S side of Pine Mt., Kings Gap Rd. 3 km E of GA-354, *S 10977*. North Carolina: Henderson Co., W of Avery Creek, Pisgah Nat'l. For., For. Rd.-479 0.1 km S of NC-2, *S 10824*. Ohio: Portage Co., Notman Rd. near Hwy.-224, *C & C 49*; Richland Co., Mansfield, Henley Rd. ca. 0.7 km W of I-71, *C & C 31*. Pennsylvania: Greene Co., PA-18 4 km SW of Holbrook, junction of Tom's Run Rd., *S 10673*.

S. lowrieanum (Porter) G.L. Nesom [*Aster lowrieanus* Porter] – $2n$ 16. U.S.A. North Carolina: Mitchell Co., NC-261 2.3 km N of Glen Ayre, *S 10816*; Watauga Co., E of village of Beech Creek, US-321 0.7 km E of McGuire Rd., *S 10796*. – $2n$ 16 + 2 supernumeraries. U.S.A. Virginia: Grayson Co., Jefferson Nat'l. For., along Cabin Creek near hairpin turn on US-58, W of For. Rd.-797, *S 10759*.

S. novae-angliae (L.) G.L. Nesom [*Aster novae-angliae* L.] – $2n = 10$. CANADA. Ontario: Lambton Co., N of Camlachie, Lakeshore Rd. 7.2 km NE of Co. Rd.-26, *S & Zh 10598*. U.S.A. Georgia: Dade Co., Tenton, along branch of Lookout Creek, near high school and GA-138, *S 11001*. North Carolina: Henderson Co., NC-280 between towns of Mill River and Avery Creek, just N of Cardinal Rd., possible "wildflower" seeding along roadside, *S 10837*.

S. ontarione (Wiegand) G.L. Nesom var. *ontarione* [*Aster ontarionis* Wiegand] – $2n = 32$. CANADA. Ontario: Essex Co., Maidstone Twp., Co. Rd.-22 W of Puce, Wallace Woods, *C & Parks 22*; Leeds Co., SW of Brockville, 1000 Islands Parkway, 0.4 km SE of Jones Creek, 0.7 km SE of Sherwood Springs Rd., *S 10655*.

S. oolentangiense (Riddell) G.L. Nesom [*Aster oolentangiensis* Riddell] – $2n = 32$. U.S.A. Florida: Gadsden Co., I-10 eastbound rest area, just E of Apalachicola R., *S 10956*. Georgia: Dade Co., SE of Trenton, NW side of Lookout Mt., GA-138 at upper hairpin turn, *S 10997*.

S. patens (Aiton) G.L. Nesom var. *patens* [*Aster patens* Aiton var. *patens*] – $2n = 20$. U.S.A. Georgia: Putnam Co., SW of Warfield, US-129 SE of Little R., 6.3 km N of GA-212, *S 10874*; Taylor Co., SE of Carsonville, old US-19 N of GA-208, 1.4 km S of Little Patsiliga Creek, 3.6 km S of Five Pts., *S 10972*; Walker Co., Chattahoochee Nat'l. For., Maddox Gap, GA-136 at For. Rd.-250, *S 10984*.

S. phlogifolium (Muhl. *ex* Willd.) G.L. Nesom – $2n = 20$. U.S.A. North Carolina: Macon Co., S of Highlands, NC-28 8.3 km S of US-64, 0.8 km N of Wilson Rd., *S 10856*.

S. pilosum (Willd.) G.L. Nesom var. *pilosum* [*Aster pilosus* Willd. var. *pilosus*] – $2n = 32$. U.S.A. Ohio: Richland Co., Mansfield, Hanley Rd. ca. 0.7 km W of I-71, *C & C 32*. North Carolina: Transylvania Co., just NE of Conestee, US-276 8 km S of US-64 (in Brevard), *S 10844*. West Virginia: Marion Co., US-250 2 km SE of Metz, *S 10683*. – $2n$ 48. U.S.A. Virginia: Wythe Co., SW of Speedwell, Iron Mt., Comers Rock, For. Rd.-57 5.5 km W of US-21, *S 10783*.

S. pilosum (Willd.) G.L. Nesom var. *pringlei* (A. Gray) G.L. Nesom [*Aster pilosus* Willd. var. *pringlei* A. Gray.] – $2n = 48$. CANADA. Ontario: Bruce Co., S of South Sauble Beach, Pashwood Dr. just E of Co. Rd.-13, *S 10669*. U.S.A. Virginia: Wythe Co., SW of Speedwell, Iron Mt., Comers Rock, For. Rd.-57 5.5 km W of US-21, *S 10784*. West Virginia: Pocahontas Co., Co. Rd.-21 10.9 km SE of Huntersville (WV-39), *S 10720*.

S. plumosum (Small) Semple [*Aster plumosus* Small] – $2n = 8$. U.S.A. Florida: Franklin Co., S of Sumatra, Apalachicola Nat'l. For., junction of For. Rd.-129 and For. Rd.-129A, 1.95 km E of FL-65, *S 10925*; For. Rd.-129A 3.2 km N of For. Rd.-129, *S 10929*. Note: This species is closely related to *S. concolor*. Both species have a chromosome base number of $x = 4$ and the virguloid type satellite chromosome (Semple et al. 1983).

S. praealtum (Poir.) G.L. Nesom var. *praealtum* [*Aster praealtus* Poir. var. *praealtus*] – $2n = 32$. CANADA. Ontario: Essex Co., Windsor, field S of Spring Garden Blvd., SE of school, *S & Zh 10604*.

S. prenanthoides (Muhl.) G.L. Nesom [*Aster prenanthoides* Muhl.] – $2n = 32$. CANADA. Ontario: Elgin Co., Hwy.-73 2.5 km W of Copenhagen, along creek S of rd., *S & Zh 10595*; Little Jerry Creek, N of Hwy.-3, *S & Zh 10591*; Little Jerry Creek, S of Hwy.-3, *S & Zh 10592*; S of Orwell, N edge of Springwater Conservation Area, *S & Zh 10588*; W of Vienna along Big Otter Creek, *S & Zh 10593*; S of Wallacetown, S of TyrConnell, small creek near Lake Erie, *S & Zh 10581*, *S & Zh 10582*. U.S.A. Ohio: Carrol Co., junction of Hwy.-43 and Belleflower Rd., *C & C 48*. Pennsylvania: Clarion Co., Hwy.-36 0.5 km S of Newmansville, *C & C 61*; Greene Co., PA-18 0.8 km S of Nettle Hill, *S 10679*; Lawrence Co., McConnelly Mill St. Pk., *C & C 53*. Virginia: Bath Co., W of Mountain Grove, VA-39 3.0 km E of WV-92, *S 10726*; Grayson Co., Jefferson Nat'l. For., along Cabin Creek near hairpin turn on US-58, W of For. Rd.-797, *S 10758*. West Virginia: Greenbriar Co., WV-39/55 just E of Nicholas Co. line, *S 10708*; Marion Co., US-250 2 km SE of Metz, *S 10680*; S of Ida May, WV-216 3.8 km S of US-250, *S 10692*; Nicholas Co., S of Birch River, Youngs Monument Rd. 0.6 km NW of US-19, along Brown's Ridge, *S 10698*.

S. priceae (Britton) G.L. Nesom [*Aster priceae* Britton] – $2n = 64$. U.S.A. Georgia: Walker Co., Davis Crossroads, cedar glade at junction of GA-193 and GA-341, *S 10988*.

S. puniceum (L.) G.L. Nesom [*Aster puniceus* L.] – $2n$ 16. U.S.A. Georgia: Banks Co., N of Commerce, US-441 1.1 km S of I-85, *S 10864*. New York: Chautaqua Co., Hwy.-474, *C & C 69*. North Carolina: Marion Co., Highlands, NC-28 0.6 km S of US-64, opposite U.S. Post Office, *S 10853*; Mitchell Co., Roan Mt., Garden Trail, S of parking lot near information booth, *S 10812*. Tennessee: Unicoi Co., S of village of Flag Pond, TN-81 N of Sam's Gap (NC border), *S 10818*. West Virginia: Nicholas Co., Summerville, WV-39 just E of US-19, *S 10707*.

S. puniceum (L.) G.L. Nesom × *S. urophyllum* (Lindl. *in* DC.) G.L. Nesom – $2n = 16$. U.S.A. North Carolina: Mitchell Co., Roan Mt., Garden Trail, S of parking lot near information booth, *S 10811*.

S. racemosum (Elliott) G.L. Nesom [*Aster racemosus* Elliott, *A. vimineus* authors not Lam.] – $2n = 16$. U.S.A. Delaware: Sussex Co., E of Georgetown, *S & Ringius 7644*. – $2n = 32$. U.S.A. Georgia: Gordon Co., I-75 N of Calhoun, south bound side rest area, *S & B. Semple 7402*.

S. retroflexum (Lindl. *in* DC.) G.L. Nesom [*Aster retroflexus* Lindl. *in* DC.] – $2n =$ 48. U.S.A. North Carolina: Henderson Co., W of Avery Creek, Pisgah Nat'l. For., For. Rd.-479 0.1 km S of NC-2, *S 10829*; Marion Co., Highlands, NC-28 0.6 km S of US-64, opposite U.S. Post Office, *S 10854*. South Carolina: Greenville Co., US-276 5.2 km S (by rd.) of entrance to Caesar's Head St. Pk., *S 10839*. Tennessee: Sullivan Co., US-421 5.8 km W of county line, *S 10769*.

S. shortii (Lindl. *in* Hook.) G.L. Nesom [*Aster shortii* Lindl. *in* Hook.] – $2n = 16$. CANADA. Ontario: Point Pelee, Co. Rd.-33 SE of Leamington, rd. side opposite lot # 914, *S & Zh 10580*. – $2n = 16 + 2$ supernumeraries. CANADA. Ontario: Essex Co., E of Colchester, Co. Rd.-50, lot #257, W of Holiday Bluff Rd., *S & Zh 10579*.

S. simmondsii (Small) G.L. Nesom [*Aster simmondsii* Small] $2n = 64$. U.S.A. Florida: Hamilton Co., SE of Jasper, US-41 2.2 km SE of West Occidental Train Station, *S 10965*.

S. tradescanti (L.) G.L. Nesom [*Aster tradescanti* L.] – $2n = 32$. U.S.A. Maine:

Penobscot Co., Old Town, rock outcrop by Stillwater R., just down stream from Gilman Falls, *Haines s.n.*

S. undulatum (L.) G.L. Nesom [*Aster undulatus* L.] – $2n = 32$. U.S.A. Georgia: Harris Co., Hines Gap Rd. 08. km, S of GA-90, F.D.R. St. Pk. near top of Pine Mt., *S 10975*. North Carolina: Henderson Co., W of Avery Creek, Pisgah Nat'l. For., For. Rd.-479 1.6 km SW of NC-2, *S 10830*. Ohio: Ashland Co., Mohican St. Pk. near Hwy.-97, *C & C 35*. Virginia: Bland Co., S of Bastian, Appalachian Trail just E of I-77, *S 10739*. West Virginia: Nicholas Co., S of Birch River, Youngs Monument Rd. 0.6 km NW of US-19, along Brown's Ridge, *S 10700*.

S. urophyllum (Lindl. *in* DC.) G.L. Nesom [*Aster urophyllus* Lindl. *in* DC.] – $2n = 16$. CANADA. Ontario: Elgin Co., Hwy.-73 2.5 km W of Copenhagen, *S & Zh 10594*. U.S.A. North Carolina: Mitchell Co., Roan Mt., Garden Trail, S of parking lot near information booth, *S 10810*.

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THIRTY-SIX YEARS OF CHANGE IN AN EASTERN HEMLOCK-WHITE PINE STAND IN WESTERN MASSACHUSETTS

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ABSTRACT. The vegetation of an eastern hemlock (*Tsuga canadensis*)-white pine (*Pinus strobus*) stand at Arcadia Wildlife Sanctuary, Easthampton, Massachusetts, was studied in 1963, in 1975, and again in 1998–99. Hemlock remained dominant from 1963 through 1999 despite extensive mortality of smaller stems. White pine and two minor canopy species, red maple (*Acer rubrum*) and black cherry (*Prunus serotina*), also declined. Changes in stem size structure of tree populations within the stand may have reflected in part increasing stand maturity, resulting in fewer and larger trees. In addition, low recruitment into the canopy and numerous tree deaths between 1963 and 1975 occurred at a time of widespread regional drought. Tree seedlings, nearly absent from the site in 1963, were well established by 1975, approximately five years after rainfall amounts returned to normal levels, but extensive mortality of canopy trees continued through 1998, particularly hemlock and black cherry. Tree deaths during this latter period coincided with defoliation by gypsy moths (*Lymantria dispar*) and wind throw during severe ice storms in the winter of 1996–1997. Hemlock wooly adelgids (*Adelges tsugae*) were not observed at the site until after the 1998 sampling; thus this study may serve as a baseline for assessing adelgid damage in the future.

Key Words: hemlock-white pine forest, *Tsuga canadensis*, *Pinus strobus*, hemlock wooly adelgid (*Adelges tsugae*)

The roles of American hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*) and their interrelationships within New England forests have been studied for more than a century. Nichols (1913, 1935) considered hemlock a characteristic tree of the "climatic climax forest" of the region and white pine a regular though minor component of this forest, with individual pine trees sometimes present as relicts of earlier stages of succession. Bromley (1935) presented historical evidence

that precolonial forests of southern New England included three distinct vegetation types, forming oak, white pine, and northern forest (hemlock-northern hardwoods) regions. In the white pine region, white pine appeared as a superdominant tree or group of trees emerging from a canopy of hardwoods (Bromley 1935; Hibbs 1982). Nonetheless Bromley agreed with Nichols that white pine-hemlock formed the climatic climax of the area.

More recent studies based on presettlement tree surveys and spatial analysis (Cogbill 2000; Cogbill et al. 2002) suggest, however, that the importance of hemlock and pine in New England was overestimated, and that within the precolonial landscape, a northern hardwood forest dominated by beech (*Fagus grandifolia*) originally was separated from a more southerly "central hardwood" forest dominated by oaks (*Quercus* spp.). Hemlock was most prevalent in the uplands, especially in Massachusetts to the west of the Connecticut River, while white pine was "remarkably uncommon" in the uplands and scarce to absent in western Massachusetts. In addition, studies based largely at Harvard Forest in Petersham, Massachusetts (Foster et al. 1992; McLachlan et al. 2000) led to the conclusion that sites characterized by hemlock with emergent white pines may give "the impression of great size and stability" but may in fact represent complex patterns of response to anthropogenic disturbance that do not reflect presettlement conditions. Previous forest composition was distinctive for each of the Harvard Forest sites and included a range of successional stages including various hardwood species as well as hemlock and white pine. Over time, forest composition at the sites converged on hemlock as a result of selective logging, wind throw, and outbreaks of pathogens such as the fungus causing chestnut blight.

A hemlock-white pine stand now included as a part of Arcadia Wildlife Sanctuary, a property owned by the Massachusetts Audubon Society in Easthampton, Massachusetts, has been studied extensively three times over a 36-year interval. The stand was first investigated during summer, 1963, by M. R. Castelli as part of a broader examination of the successional role of hemlock in the Connecticut River Valley in Massachusetts (Castelli 1964). The Arcadia site was chosen because the forest, on preliminary inspection, seemed an example of a hemlock-white pine stand that was undergoing transition to a "hemlock consociation," a geographic variant of the regional climax vegetation with only hemlock as a dominant (Oosting 1956). The stand was believed to represent a mid-successional stage and was compared with both younger and older sites. The 1963 sampling was conducted after the onset of widespread regional

drought (see Figure 1 in Holland et al. 2000, which was based on precipitation data available from the National Oceanic and Atmospheric Administration website: http://www.ncdc.noaa.gov), and tree seedlings of any species were virtually absent from the stand.

The stand was studied again during fall, 1975, by W. B. Coleman (Coleman, unpubl. ms.). By 1975, total precipitation in the area had returned to predrought levels (Figure 1 in Holland et al. 2000) and tree seedlings within the stand were abundant.

A third intensive sampling of the site was carried out during 1998–1999 by B. Garcia Bailo (Garcia Bailo, unpubl. ms.). This sampling was intended in part to document stand composition prior to an anticipated infestation by the hemlock wooly adelgid (*Adelges tsugae*), an invasive exotic insect that had already caused widespread damage to hemlocks in forests immediately to the south (Orwig and Foster 1998).

The present study is a synthesis and comparison of vegetation data from 1963, 1976, and 1998–1999. Specific goals were: (1) to identify and census each tree in the stand at each sampling period; (2) to establish the population size structure of each tree species at each sampling period; (3) to document seedling establishment and herbaceous cover at each sampling period; and (4) to attempt to determine long-term patterns of vegetational change within the stand.

MATERIALS AND METHODS

Study site. The Arcadia site is located in Easthampton, Massachusetts, on an upper Connecticut River terrace north of Mount Tom State Reservation and approximately 2000 m southwest of Hulbert's Pond, an ancient oxbow of the Connecticut River (U.S. Geological Survey, Easthampton, MA topographic map, 1964 edition). The site was acquired by the Massachusetts Audubon Society as part of Arcadia Wildlife Sanctuary in the mid-1960s. Land use prior to the establishment of hemlock-white pine forest is uncertain, although Coleman (unpubl. ms.) surmised, based on evidence from conversations with a previous owner of the site and the presence of stumps of hardwoods, including American chestnut (*Castanea dentata*) at its periphery, that it may have been an open woodland that was sporadically cut for fuel. Coleman believed disturbance had been minimal since around 1900. Through the period 1963–1999, the hemlock-white pine stand occupied approximately 0. 36 ha and was roughly oval, 100 m long and 50 m across at its widest point. Its general limits were defined by two brooks, Hemlock Brook to the

north and an unnamed brook to the south. These streams merged at the eastern margin of the site. The slippery clay banks of Hemlock Brook and a wetland surrounding the southern brook made access difficult, and thus the forest had been only slightly disturbed by human activities. The forests adjacent to the site originated on land that was cleared for agriculture through the early 1900s and were mostly cutover hardwoods in earlier stages of succession. These tracts reportedly burned prior to the beginning of the study (Arcadia Wildlife Sanctuary staff, pers. comm.) but the fires did not enter the hemlock-white pine stand.

Aside from drought, two disturbances with regional impacts may have affected the stand between 1963 and 1998–1999. Defoliation resulting from heavy infestations of the gypsy moth (*Lymantria dispar*) occurred in adjacent forests in the late 1970s and early 1980s. Vegetation studies associated with breeding bird surveys in 1994 and 1995 indicated a shift in canopy dominance after 1975 from oak species to white pine (Mooney, unpubl. ms., Arcadia Wildlife Sanctuary; Neelon, unpubl. ms., Arcadia Wildlife Sanctuary); the degree to which the moths affected the hemlock-white pine stand was not determined at the time. In addition, wind throw during two major ice storms during winter, 1996–1997, toppled a grove of hemlocks east of the Arcadia stand and caused minor tree loss in the stand itself.

White-tailed deer (*Odocoileus virginianus*) are seen regularly at Arcadia Wildlife Sanctuary, but browse effects on the vegetation were not observed in vegetation studies associated with the breeding bird survey, in studies of the herb stratum of nearby floodplain forests (Holland and Burk 1984; Holland et al. 2000), or by trained sanctuary staff (D. McLain, pers. comm.). Hemlock wooly adelgids were first observed in the stand after the 1998 sampling.

Sampling in 1963. During spring, 1963, the entire stand was divided along lines laid out with a compass to form a grid of 144 quadrats, each 5 m × 5 m. Each tree was identified to species and its diameter at 1.5 m above ground (DBH) recorded in one of six diameter size classes: 2.5–10.1 cm, 10.2–20.2 cm, 20.3–30.4 cm, 30.5–40.5 cm, 40.6 cm–58.3 cm, and 58.4 cm and larger. A map was then prepared indicating the position, identity to species, and size class of each tree. Ages of representative trees of each species in each size class were determined by counting annual rings in a core taken at 4.5 feet above ground with an increment borer. Frequency [(number of occupied quadrats ÷ total number of quadrats sampled) × 100] was determined for each herbaceous species and woody seedling in the stand.

Sampling in 1975. During fall, 1975, an attempt was made to re-locate each tree on the 1963 map, and DBH was recorded as before. A grid of 5 m × 5 m quadrats was laid out across the stand and the number of seedlings of each tree species in each of 144 quadrats was recorded. All woody stems less than 60 cm height were considered seedlings. Woody stems over 60 cm height but less than 2.5 cm diameter were considered saplings. Because this study was initiated late in the growing season, herbaceous species were listed but not sampled.

Sampling in 1998–1999. Between May and late September, 1998, another attempt to re-locate trees on the 1963 map and to measure the DBH of each tree in the stand was carried out. Snags and standing dead trees were omitted from the survey, and trees indicated on the map but not found in the stand were assumed to have fallen and decomposed or to have been removed from the site as firewood. Because tree seedlings were much more numerous than in previous sampling periods, tree seedlings were not counted throughout the entire stand. Instead, during summer, 1999, a grid of 1 m × 1 m quadrats was laid out across the stand, and tree seedlings, defined as in 1975, were counted in each of 100 quadrats placed at regular intervals along baselines through the stand in an attempt to sample all sections of the stand proportionately.

Relative dominance [(basal area of an individual species ÷ basal area of all species) × 100] and relative density [(number of individuals of a species ÷ number of individuals of all species) × 100] were calculated (Barbour et al. 1998; Mueller-Dombois and Ellenberg 1974). Basal area was determined according to Phillips (1959). Relative densities and relative frequencies [(frequency of a species × 100) ÷ sum of frequencies of all species] of tree seedlings were calculated for both the 1975 and the 1998–1999 seedling data. Frequency was also determined for each herb species occurring in the quadrats. Because determinations of frequency are influenced by quadrat size (Mueller-Dombois and Ellenberg 1974), frequency data for the smaller quadrats used in 1999 cannot be compared with prior years. Nomenclature follows Sorrie and Somers (1999).

RESULTS

Sampling in 1963. At the beginning of the study, hemlock was the dominant and most numerous canopy tree species in the stand (Table 1; Figures 1 and 2). Most hemlocks occurred in the three lower size classes (Figure 3), with nearly 40% of the trees ranging from 10.2–20.1 cm DBH. Only six hemlocks were greater than 30.4 cm in diameter. The

Table 1. Total number (n), density (stems/ha) and basal area (m^2/ha) of trees of each species and total number, density, and basal area of trees of all species present at each study period.

	Year								
	1963			1975			1998		
Species	n	Density	Basal Area	n	Density	Basal Area	n	Density	Basal Area
Hemlock	209	581	22.6	169	469	27.8	114	317	40.1
White pine	45	125	15.3	37	103	21.4	27	75	27.1
Red maple	43	119	2.3	37	103	3.5	34	94	5.8
Black cherry	15	42	0.6	11	31	0.6	3	8	0.3
TOTAL	312	867	40.8	254	706	53.3	178	494	73.3

largest hemlocks ranged from 61 to 63 years of age in 1963 and tended to cluster near the center of the site, with younger and smaller hemlocks concentrated towards the margins.

White pine, which was slightly more numerous than red maple (Table 1; Figure 1), ranked second in relative dominance to hemlock (Figure 2). White pines were better represented in the larger size classes than other tree species, with more than 40% of the trees over 30.4 cm in diameter (Figure 3). The oldest pines ranged from 57 to 68 years in age and were scattered throughout the site.

Red maple (*Acer rubrum*) occurred only in the lower size classes and black cherry (*Prunus serotina*) was a minor stand component. The largest maples ranged from 25–27 years of age, the largest black cherries from 20–29 years.

Tree seedlings and saplings were very scarce, occurring only near the stand's periphery. The herbaceous stratum was poorly developed, with most herbs occurring in patches under breaks in the canopy. The most frequent herbs were *Dryopteris carthusiana*, *Maianthemum canadense*, *M. racemosum*, *Trillium erectum*, and *Trientalis borealis*.

Sampling in 1975. Trees of all four species declined in number between 1963 and 1975 (Table 1). Because of the near absence of seedling and sapling trees in 1963, we doubt that any new stems entered the canopy size classes, but we cannot be certain this was the case. Changes in the number of individual trees within each size class may have occurred either from mortality or the transition of individual trees into or out of that size class resulting from growth. Hemlocks decreased by 19% with the highest declines in the two smaller size classes (Figure 3). White pine decreased by 18% with declines in numbers also greater

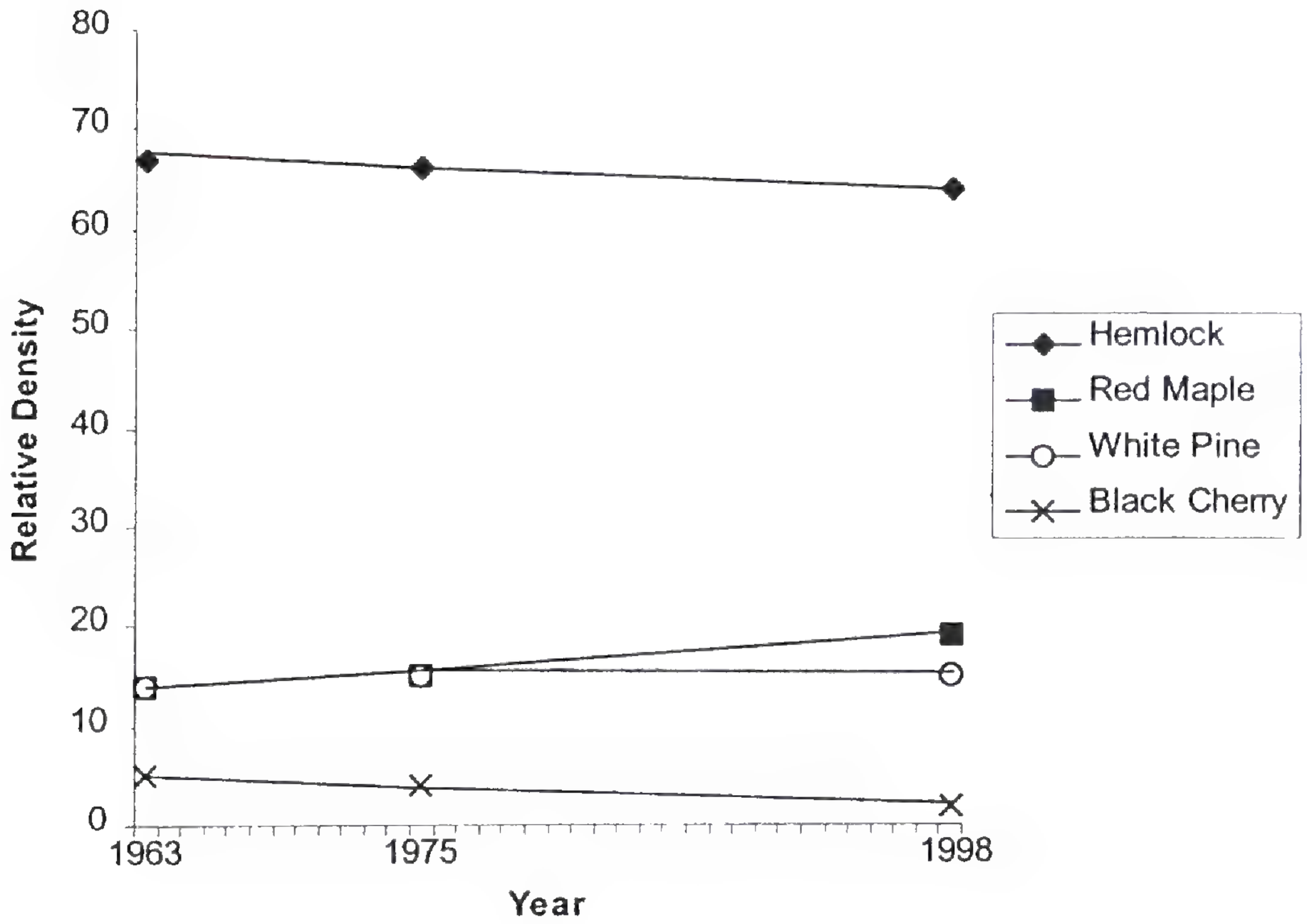

Figure 1. Relative density of each tree species at each study period.

in the two lower size classes; however the number of trees over 30.4 cm diameter rose to more than 70% of the white pine population. Red maple declined by 14% and black cherry by 27%; in both species the lower size classes sustained the greatest loss of numbers. Despite losses through mortality, basal areas of all species except black cherry increased through the period (Table 1). Tree seedlings and saplings also increased, especially near the borders of the stand, with red maple, hemlock, and black cherry particularly numerous (Table 2). White pine seedlings were still infrequent. *Lycopodium clavatum*, *Dryopteris carthusiana*, and *Mitchella repens* were the most frequent herbs, along with *Polystichum acrostichoides*, *Maianthemum canadense*, *M. racemosum*, *Trientalis borealis*, and *Aster divaricatus*.

Sampling in 1998–1999. By the end of the 36-year study period, total tree density had declined by 45% (Table 1). As in 1975, we were uncertain whether any stems had entered the canopy size classes or not. Mortality was greater in hemlock than pine, with slightly over half (55.6%) of the original number of hemlocks and three fourths (75.8%) of the original number of pines represented in the stand. Nonetheless, the relative density and relative dominance of hemlock and white pine remained essentially constant (Figures 1 and 2). Approximately two-thirds (62.8%) of the original number of red maple trees were present,

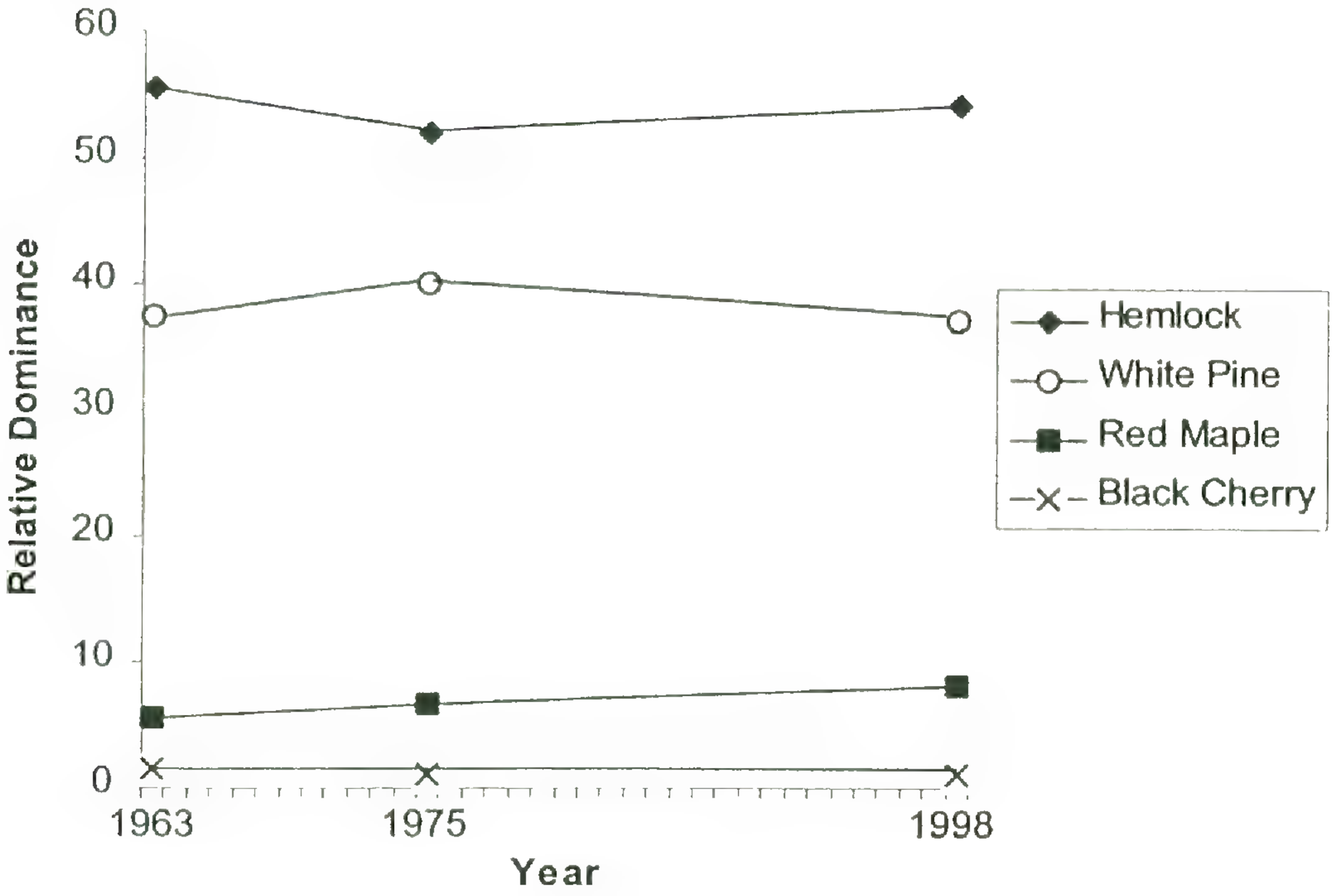

Figure 2. Relative dominance of each tree species at each study period.

but only a few black cherries persisted, most having died in the interval 1975–1998 (Table 1). During the 36-year interval, the population structure of all tree species shifted from a predominance of trees in smaller DBH classes to a predominance of trees in higher DBH classes; hence all species were represented by fewer but larger specimens (Table 1; Figure 3). Basal areas of both hemlock and white pine increased more than 75% (Table 1).

Total seedling density was over five times greater than in 1975. Red maple seedlings remained most numerous. White pine seedlings had increased, comprising over 30% of the seedling population, and surpassing hemlock seedlings in abundance. Black cherry seedlings did not occur in the 1999 sampling. While individual plants of *Dryopteris carthusiana* occurred throughout the site, the most abundant herbaceous species in 1999 was *Dennstaedtia punctilobula*, which formed colonies in several patches under light gaps. *Trientalis borealis*, *Medeola virginiana*, *Maianthemum canadense*, *Lycopodium obscurum*, *Trillium erectum*, and *Gaultheria procumbens* were also present at frequencies above 5%.

DISCUSSION

Long-term studies of vegetation at specific sites are generally scarce (Runkle 1990), although research in hemlock-white pine stands may be

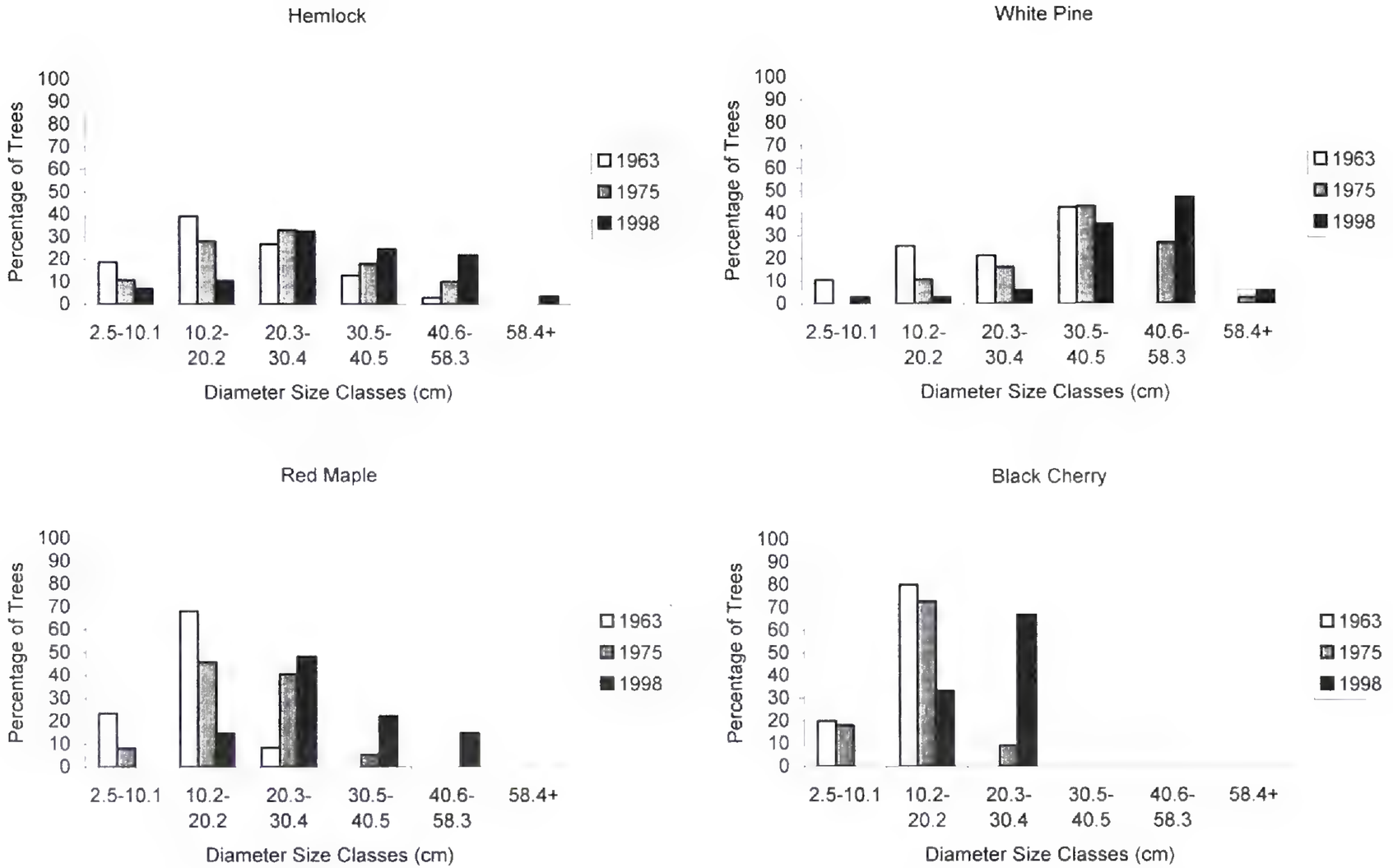

Figure 3. Percent of trees of each species represented in each of six diameter size classes at each study period.

Table 2. Density (D, stems/ha) and relative density (RD) expressed as percent of tree seedlings in 1975 and in 1998. *mostly *Quercus* spp.

	Year			
	1975		1998	
Species	D	RD	D	RD
Hemlock	822	27.5	2700	17.1
White pine	22	0.7	4800	30.1
Red maple	1392	46.6	7200	45.6
Black cherry	553	18.5	—	—
Other species*	200	6.7	1100	7.0

better represented than in most forest types. Lutz (1930), for example, described a hemlock consociation, defined by the predominance of hemlock in the larger size classes, from the Heart's Content forest in northwestern Pennsylvania. Hemlock seedlings were also abundant in these stands, which Lutz believed represented a stable "environmental or physiographic climax." Further investigations of Pennsylvania forests considered mortality of large or overstory hemlocks among the chief effects of the regional droughts of the 1930s (Hough and Forbes 1943). A reinvestigation of the Heart's Content forest in 1978, fifty years after the initial sampling (Whitney 1984) found that extensive browsing by white-tailed deer had greatly reduced hemlock seedlings and saplings but had little effect on hemlock trees, even in the smaller size classes. During the fifty-year interval, the estimated hemlock density had more than doubled to nearly 500 stems/ha. Similarly, McLachlan et al. (2000) examined four stands dominated by hemlock at the Harvard Forest, Petersham, Massachusetts in 1995, and compared them with similar adjacent plots that were sampled in 1937. By the early 20th century, the stands had moved from earlier successional hardwoods to hemlock as a result of disturbances including chestnut blight and logging. Between 1937 and 1995, the stands became "more massive" and increasingly dominated by hemlock. Within each stand, hemlock densities nearly or more than doubled during the 58-year interval, increasing to a stand average of over 1000 stems/ha, with extensive hemlock regeneration in the understory.

The history of the Arcadia site through the early 20th century may have been similar to that at Petersham. However, in contrast to trends observed at Petersham and Heart's Content, stem densities of all tree species at Arcadia declined from 1963 through 1998, with numerous tree

deaths and low recruitment of canopy trees. Over the period 1978–1986, Runkle (1990) also found very high mortality for small tree stems and lower mortalities for intermediate and larger trees in an older hemlock stand in upstate New York. He suggested that an acceleration of a previously noted decline of small stems over the eight-year interval may have resulted from browsing by white-tailed deer and the severe effects of droughts in 1982 and 1983 on younger trees.

Prolonged droughts can result in the deaths of "mesic" forest species (White 1979), especially for shallow-rooted trees such as hemlock (Hough and Forbes 1943; Runkle 1985, 1990). Tree deaths in the Arcadia stand between 1963 and 1975 coincided with the regional drought that ended in the late 1960s (Figure 1 in Holland et al. 2000). Castelli (1964) observed "few dead old trees" in 1963, but also noted the lack of seedlings and saplings in the stand and estimated that no trees had entered the canopy for at least twelve years. Coleman (unpubl. ms.) was able to census a total of 65 standing or recently fallen dead trees during fall, 1975. Of these, only six stems had diameters greater than 30.5 cm. She observed that most tree deaths occurred in the densest portions of the stand. Tree deaths between 1975 and 1998 could have resulted in part from gypsy moth damage. Although gypsy moths normally feed on deciduous tree species, primarily oaks, during large population outbreaks they may also eat needles of hemlock and other conifers (Leonard 1981). In addition, the narrow width of the stand and its position, surrounded by shorter deciduous vegetation, may have made it particularly vulnerable to wind-throw during ice storms. Whatever the cause, substantial hemlock mortality in the stand was occurring years before the arrival of hemlock wooly adelgids.

This study may serve as a baseline for assessing the effects of the hemlock wooly adelgid on regional forests. Given the discovery of adelgids at the Arcadia site after the 1998 sampling and predictions that adelgid damage will result in"unprecedented hemlock loss" throughout the entire range of hemlock (Orwig et al. 2002), the floristic composition and the size structure of the canopy trees within the stand are likely to change in the near future. In adelgid-infested stands in southern Connecticut, smaller hemlock trees suffered greater mortality than larger trees (Orwig and Foster 1998). In the Connecticut stands with moderate to high hemlock mortality, black birch (*Betula lenta*) was the most important woody invader along with red maple, black cherry, and various oaks. Similarly, Kizlinski et al. (2002) found that sites infested with hemlock wooly adelgid showed higher light levels than

undamaged sites, along with increased frequencies and cover of several components of the understory vegetation, particularly red maple and black birch.

The greatly increased numbers of seedlings of white pine, red maple, and oak in 1998–1999 at the Arcadia site, especially the higher densities of seedling white pines (Table 2), and the recent expansion in the herbaceous stratum of *Dennstaedtia punctilobula*, a fern known to spread aggressively in open wooded sites and clearings (Nauman and Evans 1993), all suggest that light levels on the forest floor have already increased. In forests adjacent to the Arcadia stand, white pine, red maple, red oak, and black birch are prominent in the canopy (Neelon, unpubl. ms.), with all but black birch well represented in the understory (Mooney, unpubl. ms.). Within the Arcadia stand, as the hemlocks are increasingly damaged by adelgids, white pine, red maple, red oak, and black birch can be expected to increase, their numbers augmented from nearby seed sources. In time, these species should replace hemlocks in the canopy. The SORTIE model of Pacala et al. (1993, 1996) has been used to predict patterns of forest succession in transition oak-northern hardwood forests in northeastern North America. The model examines the dynamics of nine potentially dominant or subdominant tree species, including hemlock, white pine, red maple, red oak, and black cherry. It shows red oak and black cherry dominant early in the sequence and hemlock and beech dominant in its final stages (Pacala et al. 1996). This and similar models may be helpful in predicting long-term change in forests similar to the Arcadia stand, where fewer tree species are present and one potential dominant may have been eradicated. In the shorter term, however, as the older white pines continue to grow in height, the stand at Arcadia may for a time resemble the precolonial forests of the region, where the pines were found as emergent or superdominant trees surrounded by a lower canopy of hardwoods (Bromley 1935; Hibbs 1982).

ACKNOWLEDGMENTS. Within the individual studies that led to this synthesis of the Arcadia data we have thanked the various individuals who have helped us in the field and elsewhere. Our debt to them now is only greater. In particular, our research would have been impossible without the encouragement and cooperation of the staff of Arcadia Wildlife Sanctuary over more than three decades; and we are particularly grateful to Robie Hubley, Judith Pierce, Mary Shanley, and David McLain for their expertise, assistance, and logistical support throughout the period.

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NEW ENGLAND NOTE

RECORDS FOR *CAREX ROSTRATA* (CYPERACEAE) IN NEW ENGLAND

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Carex rostrata Stokes is a circumboreal, hydrophytic sedge primarily restricted to Canada in North America. Its limited conterminous United States distribution includes the Great Lakes region and northwestern states (Kartesz 1999; Reznicek and Ford 2002). *Carex rostrata* has largely been treated as including *C. utriculata* Boott *in* Hook. by American authors. Fernald (1950) and Seymour (1982) provided infraspecific names for these taxa; however, the characters used in these and other treatments were inadequate to distinguish some material. As a result, many New England collections were identified only to the level of species (using the name *C. rostrata*). This has created a situation in which the name *C. rostrata* has been misapplied to collections of *C. utriculata*. Further, *C. rostrata* has been summarily excluded from New England by recent works covering this region (Gleason and Cronquist 1991; Kartesz 1999), though no systematic herbarium surveys have been performed to verify the presence or absence of this sedge in the northeastern United States. This note presents the results of recent field and herbarium surveys that have resulted in the discovery of four stations for *C. rostrata* in northern New England.

Carex rostrata and *C. utriculata* differ substantially in leaf morphology and anatomy (Reznicek and Ford 2002). However, some of the distinctions can be obscured on dried herbarium specimens (e.g., leaf color, leaf cross-sectional shape). Therefore, confident determinations rely on

presence/absence of papillae and stomate distribution on the leaves, features that require magnification to observe. These facts are likely, in part, responsible for the absence of previous reports of true *C. rostrata* in New England. As previously noted, *C. rostrata* was excluded from New England when it became customary to recognize it in the narrow sense (i.e., as separate from *C. utriculata*; Gleason and Cronquist 1991; Kartesz 1999).

The first confirmed location for *Carex rostrata* in New England was discovered by the second author and Mark Ward during field surveys of J. D. Irving property in northern Maine. The sedge was located in a backwater slough of the Big Black River, a tributary of the St. John River, in T14 R16 WELS. The section of the Big Black River that harbored *C. rostrata* is slow, tannic, and meandering with numerous oxbows that demonstrate fairly distinct zones of vegetation reflecting the degree of annual flooding. *Carex rostrata* occurred adjacent to an open pool within a mixed graminoid–shrub marsh community. Associated plant species included *C. stricta*, *C. utriculata*, *C. vesicaria*, *Sagittaria latifolia*, *S. cuneata*, *Scirpus atrocinctus*, *S. cyperinus*, and *Myrica gale*.

SPECIMEN CITATION: U.S.A. Maine: Aroostook Co., T14 R16 WELS, Big Black River oxbows, backwater emergent marsh w/ *Carex stricta*, *C. vesicaria*, *C. utriculata*, and *Calamagrostis canadensis*, 22 Aug 2002, *A. Cutko & M. Ward s.n.* (MAINE, MICH).

After learning of the discovery of *Carex rostrata* in Maine, the first author undertook herbarium surveys in regional museums in an effort to locate additional voucher specimens. This work was performed as part of the Herbarium Recovery Project, a two-year research project administered by the New England Wild Flower Society that examined herbarium records of rare and/or poorly known native tracheophytes in New England. Specimens from northern New England labeled as *C. rostrata* and *C. utriculata* were examined from GH, MAINE, NEBC, NHA, and VT. As *C. utriculata* is a relatively common sedge in New England, the herbarium surveys involved sorting through hundreds of specimens. Three collections of *Carex rostrata* were located—two from Maine and one from New Hampshire. The identifications were confirmed by Anton Reznicek (University of Michigan).

SPECIMEN CITATION: U.S.A. Maine: Aroostook Co., Ashland, Mud Pond, 17 Jul 1935, *G. Chamberlain & R. Delano 836* (NEBC); Piscataquis Co. Spencer Pond, Aug 1871, *Parlin s.n.* (NEBC). New Hampshire: Coos Co., Pittsburg, Fourth Connecticut Lake, 9 Jul 1966, *A. Hodgdon et al. 15005* (NHA).

Upon notification of a confirmed record of *Carex rostrata* in New Hampshire, the third author reexamined sedge collections from field surveys he had performed in the northern part of the state. He discovered a potential specimen of *C. rostrata* from Fourth Connecticut Lake, the site of Hodgdon's collection 23 years earlier. The specimen was examined by the first author who agreed with the initial determination (i.e., that the collection was true *C. rostrata*). Neither of the historical Maine locations have been revisited to determine if those populations of *C. rostrata* are still extant.

Fourth Connecticut Lake is a high-elevation tarn pond along the Canadian border in Pittsburg at the source of the Connecticut River (elevation 814 m). *Carex rostrata* was associated with acid to circumneutral fen and marshy emergent border vegetation surrounding the pond. The fen consisted of floating mat (pH 5.5–6.2) and mud-bottom (pH 4.6–5.0) habitats dominated by dwarf shrubs, sedges, and *Sphagnum* mosses. Common tracheophytes included *Chamaedaphne calyculata*, *Carex lasiocarpa*, *C. oligosperma*, *C. canescens*, *C. magellanica* subsp. *irrigua*, *Triadenum virginicum*, and *Rhynchospora alba*. Less frequent species included *Menyanthes trifoliata*, *Rhododendron groenlandicum*, *Eriophorum virginicum*, *Utricularia cornuta*, *Drosera rotundifolia* var. *rotundifolia*, *Dulichium arundinaceum*, *Juncus pelocarpus*, *Sarracenia purpurea*, *Carex stricta*, *Lysimachia terrestris*, and *Kalmia polifolia*. Marshy border areas contained *Gentiana linearis*, *Eleocharis palustris*, *Comarum palustre*, *Nuphar variegata*, and *Sagittaria latifolia*.

SPECIMEN CITATION: U.S.A. New Hampshire: Coos Co., Pittsburg, Fourth Connecticut Lake, 27 Jul 1989, *D. Sperduto 151* (NHA).

Carex rostrata appears to be rare and local in New England, with the sparse distribution typical of northern species of *Carex* at the southern limit of their range (Reznicek 1989). However, known collections are from relatively unspecialized habitats, suggesting this sedge may be discovered in additional locations. *Carex rostrata* has relatively narrow leaves, mostly less than 4.5 mm wide with dense and minute papillae (view at 20× or higher magnification) on the adaxial surface of the leaf blades. The stomata are usually found only on the adaxial surface (rarely some scattered on the abaxial surface in some individuals; view at 40–50× magnification; Anton Reznicek, pers. comm.). The leaf blades are white-green adaxially and U-shaped in cross-section. *Carex utriculata*, on the other hand, is marked by relatively wide leaves mostly more than 4.5 mm wide that are usually smooth on the adaxial surface. Rare

specimens will have one or more leaves covered adaxially with tiny scabrules, which provide a rough texture to the leaf. The scabrules are easily visible at 10× magnification and are more sparsely distributed than the papillae of *C. rostrata*. *Carex utriculata* is further characterized by flat or V-shaped, green leaves with stomates distributed only on the abaxial surface.

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NOTE

CONFIRMATION THAT *DIRCA* SPP. (THYMELAEACEAE) REPRODUCE FROM RHIZOMES

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There are three North American species of deciduous shrubs in the genus *Dirca* L. *Dirca palustris* L. occurs in the eastern United States and in southeastern Canada (Vogelmann 1953). Although its distribution is broad, *D. palustris* typically is obscure locally and is restricted to moist soils as an understory species along wooded slopes (Kurz 1997). *Dirca occidentalis* Gray also occurs on slopes (McMinn and Forderhase 1935), but its distribution is narrowly restricted to six counties of California near the San Francisco Bay. Within this area, *D. occidentalis* inhabits cool niches with frequent fog and relatively uniform soil moisture (Johnson 1994). *Dirca mexicana* Nesom & Mayfield was discovered in 1994 as one population of 800 to 1000 plants along a slope in the Sierra Madre Oriental of Tamaulipas, Mexico (Nesom and Mayfield 1995).

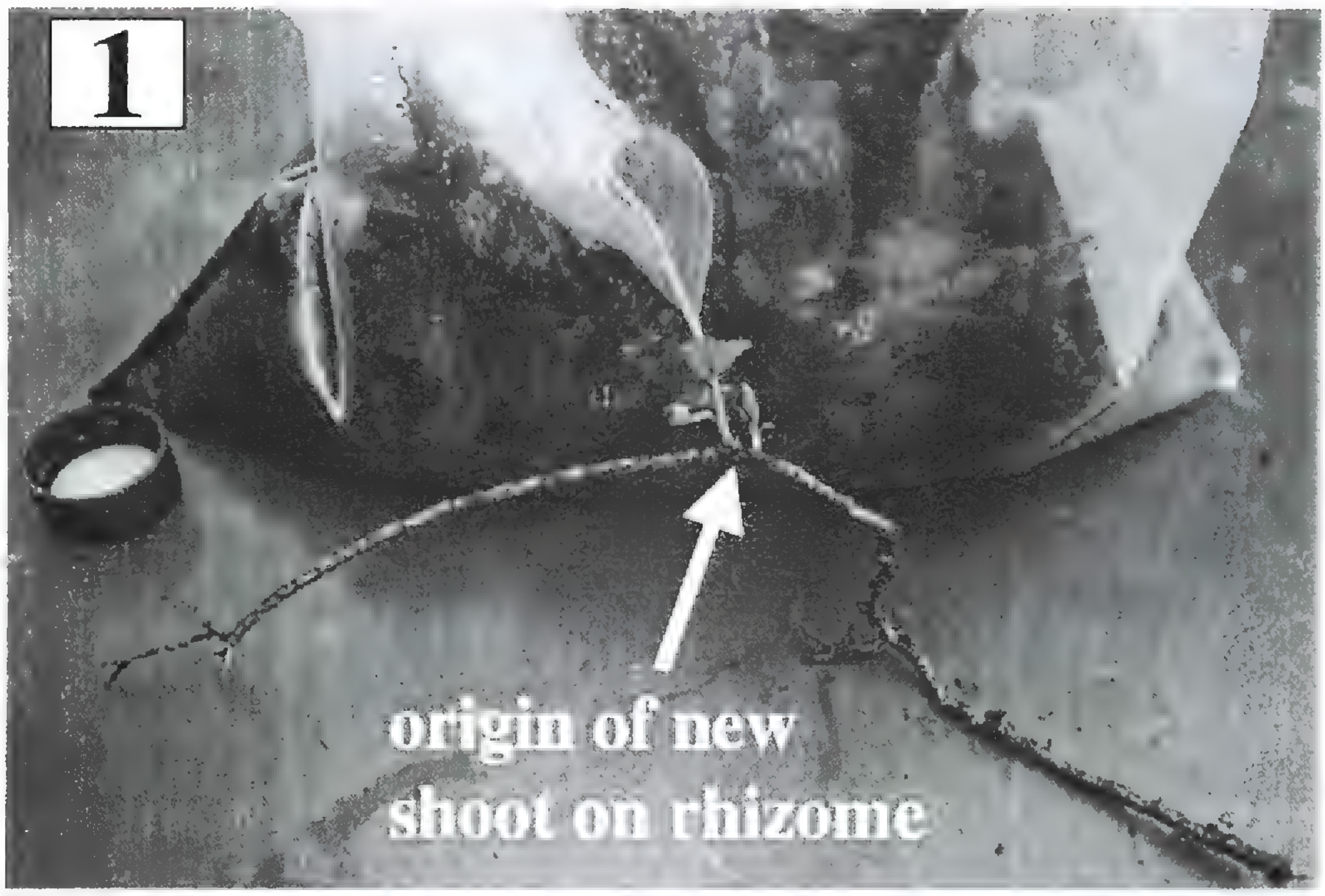
Local or global rarity of all *Dirca* spp. underscores the need to understand how these shrubs regenerate. Sexual reproduction involves the vernal development of single-seeded drupes (Vogelmann 1953). Germination rates up to 61% have been reported for *D. palustris* (Del Tredici 1983), and seedlings may develop beneath mature plants (Dirr and Heuser 1987). McMinn and Forderhase (1935) observed few fruits on *D. occidentalis*. Johnson (1994) concurred and attributed declines in populations of the species to poor fecundity, low rates of germination, seedling mortality, and competition. Nesom and Mayfield (1995) observed immature fruits on *D. mexicana* on 3 March 1995. Subsequent visits I have made to the site confirm that mature drupes with viable seeds abscise from *D. mexicana* during May.

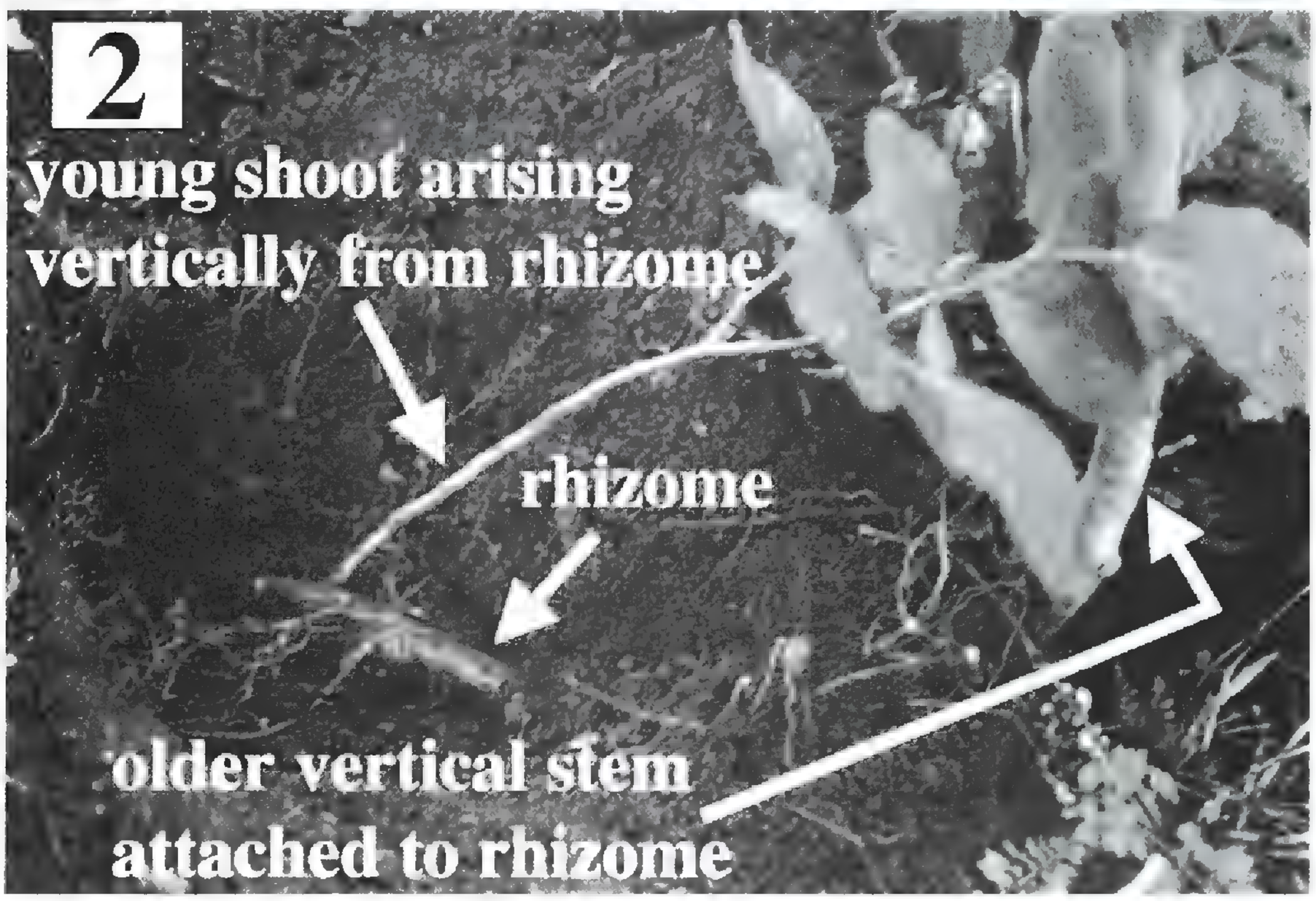
The certainty that all *Dirca* spp. regenerate sexually is contrasted by the doubt surrounding whether they spread asexually. Two modes of asexual regeneration, layering and rhizome development, are plausible based on previous descriptions of the three species in their native habitats. Stems of mature plants can become prostrate along the slopes that support populations of *Dirca* spp. Although such stems may remain

in contact with the ground for many years, adventitious root formation on prostrate stems of *Dirca* spp. has not been documented. Reports that all attempts to induce roots on stems of *D. palustris* have failed (Dirr and Heuser 1987), and that a controlled attempt to layer *D. palustris* was unsuccessful (Hendricks 1985), are additional indications that layering does not occur or is rare. McMinn and Forderhase (1935) stated that plants of *D. occidentalis* arise from "underground stems which run parallel to the surface of the ground" and that it is "difficult to find young plants . . . not connected to the parent plants." No evidence was provided for this definitive claim, nor has the possibility of rhizome development been addressed thoroughly during the ensuing 70 years. Although they did not examine the population of *D. mexicana* for rhizomes, Nesom and Mayfield (1995) stated that clonal reproduction was not evident and that the report of rhizomes by McMinn and Forderhase (1935) remained unsubstantiated. My objective for this note is to provide evidence for the regeneration of *Dirca* spp. from rhizomes.

I received permission from the Mexican and U.S. governments to import a small number of young plants of *Dirca mexicana* from the native habitat in Mexico to Iowa. Local assistants helped me to use information from Nesom and Mayfield (1995) to find the plants on 19 May 2002. Numerous newly germinated seedlings from fruits dispersed during previous years were observed. Upon excavating what appeared to be a seedling without cotyledons, I discovered it be a vertical shoot attached to a horizontal stem in the soil. A section of the rhizome was removed and photographed (Figure 1). The plant from which the rhizome had formed was not obvious, and I did not excavate further to determine the origin of the rhizome. I have observed similar regeneration of *D. palustris* at a site in Clayton County, Iowa. Figure 2 shows a young shoot that had formed from a rhizome I exposed by careful excavation on 7 June 2003. Gentle agitation of the thicker, vertical stem on the right side of the image caused the rhizome to move, indicating that both shoots in the image were attached to the rhizome.

These recent observations are evidence for clonal regeneration of *Dirca mexicana* and *D. palustris*. Considering the earlier description by McMinn and Forderhase (1935) of new plants of *D. occidentalis* from underground stems, it is likely that all *Dirca* spp. regenerate from rhizomes. The frequency of this mode of reproduction has important ramifications but is unknown. While rhizomatous spread represents a second strategy through which populations of these species can be sustained, genetic diversity likely would decrease with increases in the extent to which asexual reproduction predominates over the generation





Figures 1–2. Rhizomes of *Dirca* spp. 1. Detached segment of a rhizome of *D. mexicana*. This sample was obtained from the only known population of the species in Tamaulipas, Mexico. A new shoot that had emerged from the soil and a root attached to the rhizome to the right of the shoot are evident. 2. Rhizome at the bottom of a hole dug in the soil within a population of *D. palustris* in Clayton County, Iowa. The attachment of the younger shoot to the rhizome was observed. Agitation of the older, vertical stem on the right side of the image evoked movement of the rhizome, indicating attachment.

of new plants from seed. Those concerned with conserving *Dirca* spp. should consider that low genetic diversity may exist within populations previously presumed to have arisen exclusively through sexual means. This may be particularly relevant for the only known population of *D. mexicana* and for *D. occidentalis*, which is threatened and in decline (Johnson 1994).

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NEW BOOKS

Cycad Classification: *Concepts and Recommendations* by T. Walters and R. Osborne, eds. 2004. xvii + 267 pp. black & white illus. ISBN 0-85199-741-4 US$100.00 (hardcover). CABI Publishing, CAB International, Oxfordshire, U.K. [U.S. orders should be placed through Oxford University Press at www.oup-usa.org]

An Illustrated Guide to Eastern Woodland Wildflowers and Trees by M. Choukas-Bradley, illustrated by T. T. Brown. 2004. 424 pp. 413 line drawings. ISBN 0-8139-2251-8 $39.95 (hardcover). University of Virginia Press, Charlottesville, VA. [companion volume to the author's *Sugarloaf*: *The Mountain's History, Geology, and Natural Lore*, a guide to the plants of Sugarloaf Mountain, Maryland]

A Primer of Conservation Biology, Third Edition by R. B. Primack. 2004. xiii + 320 pp. black & white illus. ISBN 0-87893-728-5 $44.95 (softcover). Sinauer Associates, Sunderland, MA.

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NEBC MEETING NEWS

May 2004. President Art Gilman introduced this year's Distinguished Speaker, Dr. Charles Sheviak, from the New York State Museum in Albany. His talk was titled "An Orchidological Odyssey: Systematics in a Well-known Group." Chuck, who discovered his interest in botany as a fourth grader hunting for bugs, has since spent many years ironing out the wrinkles in orchid taxonomy.

His first project, which focused on populations of *Spiranthes* in the western U.S., set him off along a chain of new discoveries. Based on an old specimen from Great Basin, Utah, he located plants in Colorado that turned out to be a new species, *S. diluvialis*, intermediate between *S. magnicamporum* ($2n = 30$) and *S. romanzoffiana* ($2n = 44$). *Spiranthes diluvialis* is an allopolyploid with a chromosome number of $2n = 74$, exactly the sum of the diploid genomes from each of its parents. He later found other plants in Arizona that looked similar to *S. magnicamporum*, but turned out to be a second new species, *S. delitescens*. While looking for *S. delitescens*, he checked out reports of *S. romanzoffiana* from desert wetlands in Nevada. The plants turned out to be another new species, *S. infernalis*.

Work with the genus *Spiranthes* led him to a second orchid genus, *Platanthera*. In New York he encountered populations of two different taxa of what he referred to as "BGPs," or Basic Green *Platanthera*. Both were identified as *P. hyperborea*, though they did not appear to match the description of that species. Further investigation showed that populations in the eastern U.S. were allotetraploid ($4n$). They have since been reclassified as *P. huronensis*, which differs from other species in the genus by the higher positioning of the anthers, preventing auto-pollination. Remarkably, the eastern diploid plants were found to be from an undescribed species, now *P. aquilonis*.

Chuck has also spent a significant amount of time studying the genus *Cypripedium*, searching in particular for species that look similar to our native Lady's Slipper, but that have unique flower coloration. He has found three varieties of *C. parviflorum* so far, but notes that there is still much to be resolved in the taxonomy of this species. The most widespread, var. *pubescens*, can be highly variable in shape and size, the result of both phenotypic and genotypic variation. A second variety, originally known as var. *parviflorum*, has since been renamed var. *makasin*. It can be recognized by its small-flowered plants, found in fens, that have a distinct, fruity scent. Chuck found that they were quite unlike the true var. *parviflorum*, a southeastern species with a different

floral spotting pattern and a faint, rose-like scent. His favorite *Cypripedium* species is *C. montanum*, native to the Pacific Northwest. It hybridizes with *C. parviflorum* to form *C. ×columbianum*. Molecular studies showed that there was gene flow between the two parent species in the distant past. Interestingly, there is also current hybridization due to habitat destruction caused by logging, permitting *C. parviflorum* to move into the more montane habitat of *C. montanum*.

Chuck's studies have taken him as far as Vladivostok, near the Pacific coast of Russia. There, he found *Cypripedium macranthos* and *C. calceolus* crossing to create a series of hybrids that show all of the characters of the North American *C. parviflorum* complex. This suggests that the origin of *C. parviflorum* could have been from an ancient hybridization event that took place in Asia. Chuck found a 1:1 correlation in morphology and color patterns between the Vladivostok hybrids and *C. parviflorum* var. *pubescens*; only the intensity of the coloration varied. The variation in *C. parviflorum* var. *pubescens* may be an expression of an ancient hybrid progenitor.

Chuck ended his talk with some beautiful images of *Platanthera leucophaea* (Eastern Prairie Fringed Orchid), a very rare species. He collected specimens from Illinois and North Dakota, noting that the western plants had fewer but larger flowers. Growing them together, Chuck was surprised when the Illinois and North Dakota plants both flowered on the same day, allowing him to make a precise comparison. He noted that though the plants are both pollinated by sphingid moth species, their flowers are structured so that they each place their pollinarium on a different part of the moth. This ensures that there is no cross-pollination between the two flower types, an indication that the plants are in fact separate species. Chuck described the more western plants from the Missouri River drainage and northward as *P. praeclara*, the Western Prairie Fringed Orchid.

—Jennifer Forman Orth, Recording Secretary.

May 23–26, 2004 Southern Appalachian Field Trip. Members of the NEBC and the Southern Appalachian Botanical Society (SABS) held a joint field meeting at the Valle Crucis Conference Center in Valle Crucis, North Carolina. The group divided each day and collectively completed at least three different botanical rambles on each of the three days. The assembled group of NEBC and SABS members were kept well fed and comfortable by the staff of the Valle Crucis

Conference Center. The nightly happy hour before the early dinner was, unfortunately, often missed by botanists who dallied too long on the trails! Evening speakers Edward Schell, Dan Pittillo, and Peter White provided beautiful images of endemic plants, an introduction to the ecology of the region, and interesting new data on the glacial and post-glacial distribution of plant communities in the Southern Appalachians, respectively. The final evening was devoted to identification workshops with Lisa Standley and Bruce Sorrie co-leading one on sedges while Alan Weakley and Zack Murrell helped others with any non-sedge vascular plant identifications. The following accounts reflect the highlights of the woods in the vicinity of the Inn, as well as three of the daily outings, with an admitted bias toward sedges.

Valle Crucis Inn—The group discovered rich woods behind the Valle Crucis Inn, which provided some of the best botanizing of the trip. Thickets of *Rhododendron maximum* and *R. calendulaceum* were under a canopy of *Tsuga canadensis*, *Liriodendron tulipifera*, *Acer saccharum*, *A. rubrum*, *Quercus rubra*, *Robinia pseudoacacia*, and *Magnolia fraseri* (in bloom). These woods held a nice diversity of herbaceous species. Some of the taxa in bloom included *Aplectrum hyemale*, *Panax quinquefolius*, *Conopholis americana*, *Orobanche uniflora*, *Houstonia purpurea*, *Sedum ternatum*, *Listera smallii*, *Clintonia unbellulata*, *Salvia lyrata*, *Hydrangea arborescens*, *Coreopsis major*, *Gillenia trifoliata*, *Viola rotundifolia*, *V. hastata*, and *Aristolochia macrophylla* (with pipevine swallowtails). The trails and grounds of the inn also provided good birding.

Day 1, Roan Mountain—Alan Smith led a long, leisurely hike up the grassy bald at Roan Mountain, ending in a rocky heath bald. The grassy bald areas were dominated by *Carex pensylvanica* and *C. brunnescens*, with *C. debilis*; not by grasses! The trail crossed through some interesting patches of spruce-fir-*Sorbus* woods with *Ribes glandulosum* and *Cardamine clematitis*. The grassy balds themselves had few flowering species at this time of year (*Erythronium umbilicatum*, *Anemone quinquefolia*) but leaves and developing shoots of other species held promise of exciting swathes of bloom later in the summer, dominated by *Angelica triquinata*, *Solidago glomerata*, *S. roanensis*, and *Lilium grayi*. Heath areas were dominated by *Rhododendron catawbiense* and *R. carolinianum*, not yet in bloom. Among the many shrubs of *Vaccinium* we found *V. erythrocarpum*, a highbush blueberry with a cranberry flower. At the rocky outcrop we found leaves of the rare endemic *Geum radiatum* and cushions of blooming *Leiophyllum buxifolium*. High-elevation birds were also common in the woods and shrub thickets.

Day 2, Bluff Mountain—Alan Weakley and Jamey Donaldson led two groups to Bluff Mountain, a Nature Conservancy preserve. Bluff Mountain is a flat plateau bordered by rocky cliffs and outcrops above a rich, sloping, deciduous woods. The lower woods were dominated by maple, ash, and yellow birch with a variety of spring ephemerals just past flower (*Cardamine*, *Dicentra*, *Claytonia*, *Laportea*, *Asarum*, and *Viola* spp.) while the woods on the plateau were dominated by red and white oak, buckeye, and stands of *Tsuga caroliniana* on the edges of cliffs. The varied habitats (rock outcrops, meadows, dry heath/oak woods, rich woods, seeps and fens) gave the group a wonderful look at diverse and rare plants. In the heath areas, *Rhododendron catawbiense* was just starting to bloom. *Menziesia pilosa* was a highlight of the shrub heaths. In the more mesic woods on top of the plateau we found a new (to us) *Trillium*, *T. sulcatum*. Meadows were in bloom with *Iris cristata*, carpets of vivid orange *Castilleja coccinea*, *Senecio aureus*, and vividly magenta *Geranium maculatum* (not our northern pale pink). A seep held *Cypripedium parviflorum*. Cliffs were covered with leaves of *Geum radiatum*, the rare and spectacular *Carex misera*, *Phlox subulata*, *Houstonia montana*, *Saxifraga michauxii*, and *Asplenium montanum*. *Paronychia argyrocoma* was abundant, to the delight of Alice Schori, who has searched for it in New Hampshire. Wet meadows were dense with several species of *Liatris* (including the rare *L. helleri*) and gentians, likely to be spectacular later in the season. A large fen dominated by sedges (*Carex*, *Cladium mariscoides*, *Eleocharis*, *Eriophorum*) revealed a patch of *Carex aquatilis*, not previously recorded in North Carolina. *Carex roanensis*, another rare endemic, was abundant along road edges in the lower wooded slopes.

Day 3, Grandfather Mountain—Jamey Donaldson led a small but intrepid group from the summit of Grandfather Mountain along the Profile Trail, to the base of the mountain. The steep and rigorous scramble over rocky summits, up rock chutes, and under huge boulders was often aided by ladders and fixed ropes. Despite the 50 mph winds, the group enjoyed wonderful views and great plants. The rocky cliffs along the ridge had abundant patches of *Carex misera*, large billows of *Leiophyllum buxifolium* in flower, and tussocks of *Trichophorum caespitosum* clinging to the cliff faces. On the lower slopes of the mountain we found large patches of *Diphylleia cymosa* in bloom, along with *Saxifraga careyana*, *Viola canadensis* (pink, rather than white), and *Hydrophyllum virginianum* with vivid, deep purple flowers. Understory plants included *Aconitum*, *Coreopsis*, *Rudbeckia laciniata*, *Laportea*, *Dioscorea*, *Phlox*, *Claytonia*, *Dicentra*, *Allium tricoccum*,

Dentaria, *Trillium grandiflorum* and *T. erectum*, and *Viola* species. *Cymophyllus fraseri* and *Carex plantaginea* were highlights of the lower trail. At the base of Grandfather Mountain, we paid our respects at the two historical markers honoring famous botanists who visited the mountain: André Michaux and Asa Gray.

—Lisa A. Standley.

May 2004. Council member Ray Angelo introduced the evening's speaker, Dr. Jim Hinds. A former neuroscientist and present accountant from Orono, Maine, Dr. Hinds became interested in lichens through courses at Eagle Hill Biological Station. These initial courses have led him to wide-ranging studies in New England, which were the topic of his talk "New England Lichens: Ecology, Distribution, and Changes in Abundance During the Last 100 Years"

Dr. Hinds began his talk with a review of different lichen groups, including crustose (closely adherent to rock), foliose (attached by rhizees on their lower surface), squamulose (a few mm in size and often growing on other lichens), fruticose (stick into the air and have no differences on their two surfaces), and hanging lichens. Lichens also fall into two major groups based on their fungi: ascomycetes and basidiomycetes. The lichen form evolved two separate times, once from each group of fungi. Most lichens in New England are ascomycetes.

Ecologically, lichens are very important. Lichens colonized land about 1.2 billion years ago and were the only group on land until the mosses arrived. Dr. Hinds hypothesized that they may have affected global levels of CO_2 and O_2 and thus facilitated life on Earth. Lichens help with soil formation from bare rock due to mechanical effects of their hyphae working in the interstitial spaces of rocks. Historically, lichens were important in nitrogen fixation, particularly in alpine areas, on calcareous rocks and soils, and in old-growth forests. For example, in the Pacific Northwest, *Lobaria* species fix over 50% of nitrogen in old-growth forests. Lichens are also important in food chains, serving as food for invertebrates, flying squirrels (spotted owl food), boreal red-backed voles, white-tailed deer, and caribou.

Humans have used lichens in many ways, but most importantly as old-growth forest indicators and as biomonitors of air pollution. Lichens are particularly sensitive to SO_2. Zone charts have been developed for New England and the British Isles, where, by using lichen indicators, scientists can determine the amount of air pollution in a specific location. In New

England, sensitive lichens are most common in Maine, where they are least affected by air pollution coming from midwestern states.

As a result of comparisons Dr. Hinds has made with the well-known lichen flora of the British Isles, he feels that the macrolichens (all but the crust lichens) are well known in New England since there are similar numbers in each geographic region. The known crust lichens in New England, however, are about half the numbers known from the British Isles and more field work is needed to adequately inventory these species. He ultimately expects that lichen species numbers will be about 2/3 that of vascular plants in New England.

Macrolichens were well studied in New England in the 1800s and more recently since 1980. Dr. Hinds has compared state distributions of lichens from these two periods and has noticed some interesting trends. Eighteen species of macrolichens once found in three or more states are now found in none. Thirteen of these are sensitive to air pollution, particularly the nine species of cyanolichens (lichens that host cyanobacteria). Among the 40 species that are absent in three states or more, 21 are cyanolichens and 18 are old-growth indicators. For all but three of these species, Maine is one of the remaining states where the lichens are found, which is most likely attributable to its higher air quality. For New England in general, three species of macrolichens are historic, two species are G1 (five or few locations), six species are G2 (20 or few locations), and 10 species are G3 (100 or fewer locations). Two hundred and sixty species of New England macrolichens (57%) are considered to be rare or declining.

Over the past three years, Dr. Hinds has had a rare opportunity to be part of a collecting team for lichens and mosses on Mt. Katahdin. Through this field inventory, they have discovered nine lichen species new to North America, 31 species new to New England, 18 species new to Maine, and 93 species new to Mt. Katahdin. Many of these species are crust lichens that are hard to collect and thus have been under-surveyed in the past. Dr. Hinds concluded his talk by commenting that the results of intense surveys, such as that undertaken on Mt. Katahdin, demonstrate that there is much to be discovered with an increase in effort. Also, more studies are needed on lichen floristics, ecology, and distribution. He encouraged the audience to switch from studying vascular plants to lichens in order to do new and interesting work!

—Karen B. Lombard, Recording Secretary, *pro tempore*.

ANNOUNCEMENT

NEW ENGLAND BOTANICAL CLUB GRADUATE STUDENT RESEARCH AWARD

The New England Botanical Club will offer up to $2000 in support of botanical research to be conducted by graduate students in 2005. This award is made annually to stimulate and encourage botanical research on the New England flora, and to make possible visits to the New England region by those who would not otherwise be able to do so. It is anticipated that two awards will be given, although the actual number and amount of awards will depend on the proposals received.

The award will be given to the graduate student(s) submitting the best research proposal dealing with systematic botany, biosystematics, plant ecology, or plant conservation biology. Members of the NEBC will be given preference if competing proposals are judged to be of equal merit. Papers based on the research funded must acknowledge the NEBC's support. Submission of manuscripts to the Club's journal, *Rhodora*, is strongly encouraged.

Applicants must submit three paper copies of each of the following: a proposal of no more than three double-spaced pages, written in a scientific format with a stated hypothesis; a single page of literature cited; one-page budget with brief justification; and curriculum vitae. Two letters in support of the proposed research, one from the student's thesis advisor, should be sent directly to the Awards Committee by sponsors. All materials should be sent to: Graduate Student Awards Committee, The New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138-2020. Reference letters, but not proposals, may be sent by e-mail or FAX to the committee chair, who is listed on the NEBC Committees web page. Proposals and supporting letters must be received no later than March 1, 2005. The recipient(s) will be notified by April 30, 2005.

The Graduate Awards Committee is pleased to announce that the 2004 award has been given to Krissa Skogan of the University of Connecticut for her proposal "Using demography, genetic diversity, and the effects of increased nitrogen deposition to understand the decline of *Desmodium cuspidatum* (Fabaceae)." For an abstract of the research proposal and a listing of the awards from 1985 to the present, consult the Club's web page (http://www.huh.harvard.edu/nebc/).

ANNOUNCEMENT

MERRITT LYNDON FERNALD AWARD

The Council of the New England Botanical Club honors Merritt Lyndon Fernald's exemplary contributions to the botany of northeastern North America through the Merritt Lyndon Fernald Award. The award is given annually, if deemed appropriate, to the author(s) of the best paper published in each volume of *Rhodora* that has made use of herbarium specimens and/or involved fieldwork. Topics to be considered include, but are not limited to, biogeography, floristics, life-history studies, monographs, and revisions. Papers on vascular or nonvascular plants, lichens, fungi, and algae will be considered. The competition is not limited to a particular geographic area, but is open to studies in any part of the world. Recipients of the Fernald Award will receive $1000.00 and a certificate acknowledging the achievement. The award will be presented when the New England Botanical Club hosts its annual Distinguished Speaker.

This year's recipients of the Merritt Lyndon Fernald Award are Arthur C. Mathieson, Clinton J. Dawes, Larry G. Harris, and Edward J. Hehre for their paper entitled "Expansion of the Asiatic green alga *Codium fragile* subsp. *tomentosoides* in the Gulf of Maine" (*Rhodora* 105: 1–53. 2003). The Award Committee chose this paper as an outstanding example of the spirit of the Club's mission. The winning paper reflected use of field and herbarium data to track the invasion and spread of an Asiatic green alga from two initial colonization sites as well as subsequent introductions in the northwest Atlantic. Their discussion considered rate of spread, introduction vestors, dispersal from sites of introduction, and viability and abundance of current populations at sites with different exposure and hydrology. They also discussed two species (a red alga and a bryozoan) that have spread due to their association with *Codium*. The team of authors reflects a cross-disciplinary collaboration. In addition to being a comprehensive study and highlighting the value of field work and herbarium collections, the topic is timely in dealing with an invasive species.

THE NEW ENGLAND BOTANICAL CLUB

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THE GENUS *PHYSALIS* (SOLANACEAE) IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT. Keys and descriptions are presented for the 16 species of *Physalis* (Solanaceae) commonly found growing without cultivation in the southeastern United States, as well as for two cultivated species that sometimes escape and persist in disturbed habitats. The study was initiated as part of the Southeast Flora Project, and will ultimately be incorporated into the treatment of the genus for the *Flora of North America*.

Key Words: *Physalis*, Solanaceae, southeastern United States, floristics

The treatment of *Physalis* (Solanaceae) for the southeastern United States was written originally in the early 1980s as a contribution to the Southeast Flora Project, based at the University of North Carolina in Chapel Hill. The ultimate goal of the project was the publication of a revised and updated *Vascular Flora of the Southeastern United States*. In the mid-1980s, the Flora North America Project (FNA) was launched, and many state and regional flora projects were put aside in anticipation of a larger, more comprehensive *Flora of North America*. Although several volumes of this work have been published to date, the volume in which the Solanaceae is to be included will not be in print for several years.

More than a decade ago, the Solanaceae editor for the Southeast Flora Project encouraged me to publish my keys and descriptions of southeastern *Physalis* in order to make the treatment widely available. Since the first draft of this treatment was prepared, I have examined and annotated many additional specimens as part of my research for the Flora North America Project. In addition, some questions pertaining to issues of nomenclature have been resolved. The draft of the original document had been circulated to colleagues in the southeastern U.S., and some of their suggestions have been incorporated, as well. It is my hope that this publication will elicit constructive feedback on the utility of the work for systematists, ecologists, and field biologists, as well as encouraging research on some of the taxa that remain problematic.

For the purpose of the Southeast Flora Project, the southeastern U.S. was defined as encompassing the forested region west to the prairie and north to the terminal moraines. Thus, the region includes Delaware, Maryland, Virginia, North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, Arkansas, Tennessee, Kentucky, and West Virginia, with notation of presence in the adjacent states of Texas, Oklahoma, Missouri, Illinois, Indiana, Ohio, Pennsylvania, and New Jersey (from the *Revised Contributors' Guide for the Vascular Flora of the Southeastern United States*, January 1981). As described by the editorial board in the goals of the project, the treatment presented here includes keys, descriptions, habitat and distributional data, and pertinent synonymy for all species of *Physalis* growing without cultivation in the southeastern U.S. It is based entirely on herbarium material borrowed from AUA, CLEMS, DUKE, FLAS, FSU, GA, KNK, LSU, MARY, MEM, MISS, MUR, NCSC, NCU, NLU, PH, SMU, TENN, UARK, UNA, USCH, USF, VPI, and WVA during the early 1980s, specimens borrowed from additional herbaria as part of FNA, and new collections and field observations of the author.

Two non-native species have been included in the key, and full descriptions have been provided. Because the members of *Physalis* are "weedy" and tend to occur in disturbed habitats, it may be difficult for the collector to determine whether a plant is native or not. Both *P. alkekengi* (Chinese Lantern Plant) and *P. philadelphica* (Tomatillo) were represented in herbaria in low numbers, however collection label data indicated that the plants were established and persisting in thickets, fence rows, and along streambanks as well as more obviously cultivated ground such as yards and edges of cultivated fields. Another species, *P. peruviana* L. (Cape Gooseberry) was not included because it was seen only from garden collections and apparently either does not escape or does not persist outside of cultivation. *Physalis peruviana* would be most easy to confuse with *P. heterophylla* except that, in the former species, plants do not become decumbent nor are they glandular, the pedicels are shorter (6–8 mm vs. 9–20 mm in flower;13–15 mm vs. 20–30 mm in fruit), the anthers are usually blue or blue-tinged, and the filaments are slender.

Two additional species were not included in the key because only a few collections were seen that were weeds in cultivated fields or weeds persisting in previously cultivated ground. The first, *Physalis acutifolia* (Miers) Sandwith, is native to the southwestern U.S. and looks most similar to *P. angulata*. Vegetatively, it can not be distinguished from the narrowest-leaved representatives of that species, even in the field. *Physalis acutifolia* is distinctive in having flowering pedicels 15–40 mm long, a widely flaring corolla limb, and a slightly smaller fruiting calyx that is

nearly filled by the mature berry. *Physalis acutifolia* was seen as only a few collections from a previously cultivated area in Mississippi. The second species, *P. lagascae* Roem. & Schult., is native to the Neotropics. Several collections were seen from Louisiana and Mississippi that were weeds in sugarcane fields or associated areas. *Physalis lagascae* is an annual; the main stem is often decumbent and the lower branches trail along the ground; the leaves are small (2–4 cm long, 0.5–2 cm wide), sparsely pubescent to glabrate, ovate, with entire or irregularly dentate margins; the flowers are small (calyx 3–4 mm long; corolla 4–7 mm long) and have short pedicels (2–5 mm long); the fruiting calyx is small (1–2 cm long, 1–2 cm wide), 10-angled, rounded at base, with a short pedicel (3–6 mm long).

Some *Physalis* species are geographically wide-ranging and have a high degree of morphological variation. For *P. heterophylla* and *P. pubescens*, this variation has been recognized taxonomically (e.g., Small 1933; Waterfall 1958); those varieties have not been recognized here because they could not be correlated with environmental or geographic factors. More detailed study may result in a better understanding of the basis of variation in these taxa. Comprehensive studies of some other taxa, involving a combination of field, herbarium, and laboratory analyses, have resulted in increased insight and revised taxonomy (Hinton 1970, 1976; Sullivan 1985). Because floral morphology is fairly uniform in the genus, where related taxa occur in close proximity hybridization may occur (Hinton 1975; Sullivan 1984, 1985).

In the following treatment, all descriptions have been generated from herbarium specimens and field work. Physiographic provinces are given as follows: Coastal Plain (including Atlantic C.P., Gulf C.P., and Mississippi Embayment), Piedmont (including Piedmont Plateau and Interior Low Plateau) and Mountains (including Blue Ridge, Ridge and Valley, Cumberland Plateau, Allegheny Plateau, Ozarks, and Ouachitas), as outlined in the *Revised Contributors' Guide for the Vascular Flora of the Southeastern United States*, January 1981 (their designations follow Fenneman 1938).

PHYSALIS L., GROUND CHERRY

Annual or rhizomatous perennial herbs. Stems erect or weakly decumbent; branched; glabrous to densely pubescent. Leaves simple, alternate or falsely opposite. Leaf blade lanceolate to broadly ovate; glabrous to densely pubescent; apex acuminate to blunt; margins entire to dentate; base unequal, truncate-cordate to rounded-attenuate; petiolate or sessile. Flowers perfect; radially symmetrical; in all but one species

solitary in leaf axils; pedicellate; pendant. Calyx campanulate; enlarged and inflated in fruit, becoming reticulate-membranous and bladder-like, completely enclosing the berry; lobes 5, connivent, scarcely enlarged in fruit. Corolla 5-angulate or obscurely 5-lobed; yellow or white, often with 5 darker spots or smudges in the throat; campanulate-rotate; plicate in bud. Stamens 5; yellow, blue, or tinged blue or purple; inserted near the base of the corolla tube; anther sacs opening longitudinally. Ovary 2-celled; style elongate, slender; stigma minute. Fruit an edible, juicy berry; green, orange, or purple; in all but one species enclosed within the inflated fruiting calyx. Seeds numerous; light brown; reniform, flattened; surface finely pitted; ca. 2 mm long.

About 75 species worldwide, primarily in the Neotropics. Species boundaries are sometimes poorly defined. Some specimens are difficult to determine from preserved material, and field knowledge of the plants is essential. Several species are cultivated for ornament or food; garden escapes can persist for several years.

KEY TO SPECIES OF *PHYSALIS* IN THE SOUTHEASTERN U.S.

1. Flowers 2 or more per leaf axil; berries with spherical seed-like bodies among the flattened, reniform seeds . . . . . 1. *P. carpenteri*
1. Flowers solitary in leaf axils; berries with flattened, reniform seeds only . . . . . (2)
2. Fruiting calyx red, retaining color on drying; corolla white . . . . . 2. *P. alkekengi*
2. Fruiting calyx green or orange, drying brown; corolla yellow, often with 5 large spots or smudges in throat . . . . . (3)
3. Anthers strongly coiled after dehiscence, blue; corolla throat tinged blue; berry the size of a cherry tomato or slightly larger, pale green or purple-streaked . . . . . 3. *P. philadelphica*
3. Anthers not coiled after dehiscence, yellow, blue, or purple; corolla throat purple, brown, green, or ochre; berry small and orange, yellowish or green . . . . . (4)
4. Leaves glabrous or nearly so . . . . . (5)
5. Flowering calyx typically 6 mm or more long; perennial from deeply buried rhizome . . . . . (6)
6. Pedicel glabrous or rarely sparsely pubescent with dendroid-stelliform hairs; leaves sessile, blade narrowly spathulate to linear-lanceolate . . . . . 4. *P. angustifolia*
6. Pedicel sparsely pubescent with unbranched, antrorse hairs; leaves petiolate, blade broadly

ovate to broadly lanceolate . . . . . .
. . . . . 5. *P. longifolia*

5. Flowering calyx typically 6 mm or less long; annual from taproot . . . . . (7)

7. Corolla throat with 5 large, dark purple-black spots or smudges, visible through the dried, pressed tissue; fruiting calyx sharply 5-angled . . . . (8)

8. Leaf margin entire or dentate with fewer than 8 teeth per side; fruiting pedicel 15 mm or less long . . . . . 6. *P. pubescens*

8. Leaf margin dentate with 8 or more teeth per side; fruiting pedicel mostly 15 mm or more long . . . . . 7. *P. cordata*

7. Corolla throat yellow or only tinged purple; fruiting calyx 10-angled . . . . . (9)

9. Calyx and young stems with glandular hairs; flowering pedicel 4–7 mm long; fruiting pedicel 5–10 mm long . . . . . .
. . . . . 8. *P. missouriensis*

9. Calyx and young stems glabrous or sparsely pubescent with non-glandular hairs; flowering pedicel 7–17 mm long; fruiting pedicel 15–30 mm long . . . . . 9. *P. angulata*

4. Leaves pubescent . . . . . (10)

10. Hairs forked, 2–3 branched, or dendroid-stelliform, in some species intermixed with simple hairs . . . . .
. . . . . (11)

11. Calyx hispid; hairs stiff, 2–3 branched intermixed with unbranched, at least some of which are as long as 1–1.5 mm long . . . . . 10. *P. pumila*

11. Calyx tomentose or sparsely pubescent; hairs soft, branching 3 or more times, less than 1 mm long, sometimes intermixed with soft, 2–4 mm long, branched or unbranched hairs . . . . (12)

12. Flowering calyx and abaxial leaf surface white-tomentose, hairs obscuring plant surface or nearly so; hairs branched, 1 mm or less long, in some populations intermixed with 2–4 mm long, branched or unbranched hairs on the stem and calyx . . . . . 11. *P. mollis*

12. Flowering calyx and abaxial leaf surface sparsely to densely pubescent, hairs not obscuring plant surface; hairs branched, 1 mm or less long only . . . . . (13)
13. Anthers 1.5× or more longer than the mature filaments; fruiting pedicel mostly 1.5× or more longer than the fruiting calyx; leaf margin dentate, sinuate, or entire . . . . . 12. *P. cinerascens*
13. Anthers equal to or shorter than the elongated filaments; fruiting pedicel mostly equal to or shorter than the fruiting calyx; leaf margin entire . . . . . 13. *P. walteri*

10. Hairs all unbranched . . . . . (14)
14. Flowering calyx typically 6 mm long or less; annual from taproot . . . . . (15)
15. Corolla throat with 5 large, dark, purple-black spots or smudges, visible through pressed, dried tissue; fruiting calyx sharply 5-angled . . . . . (16)
16. Stems glabrous or sparsely pubescent with appressed, non-glandular hairs; fruiting calyx glabrous . . . . . 7. *P. cordata*
16. Stems densely viscid-pubescent with divergent hairs to almost glabrous; fruiting calyx pubescent . . . . . (17)
17. Leaf blades gray-green, drying orange or with orange patches, margins dentate; pubescence 0.5–1 mm on stems, glands sessile or short-stalked . . . . . 14. *P. grisea*
17. Leaf blades green, drying green, margins entire to dentate; pubescence less than 0.5 mm, glandular or not . . . . . 6. *P. pubescens*

15. Corolla throat yellow or only tinged purple; fruiting calyx 10-angled . . . . . (18)
18. Calyx and young stems sparsely to densely pubescent with intermixed glandular and non-glandular hairs; flowering

pedicel 4–7 mm long; fruiting pedicel 5–10 mm long . . . . . 8. *P. missouriensis*

18. Calyx and young stems glabrous or only sparsely pubescent with non-glandular hairs; flowering pedicel 7–17 mm long; fruiting pedicel 15–30 mm long . . . . . 9. *P. angulata*

14. Flowering calyx typically 6 mm long or more; perennial from deeply buried rhizome . . . (19)

19. Leaf blade broadly ovate to sub-orbicular; base rounded truncate, or sub-cordate; plants glandular or non-glandular . . . . . (20)

20. Stems densely villous, hairs divergent, 1–2 mm long, often intermixed with shorter glandular hairs; rhizomes stout and deeply buried . . . . 15. *P. heterophylla*

20. Stems glabrous to villous, hairs appressed, shorter than 1 mm, sometimes intermixed with 1–2 mm long, divergent hairs or shorter glandular hairs; rhizomes slender and typically shallow . . . . . 16. *P. arenicola*

19. Leaf blade narrowly ovate to broadly lanceolate or oblanceolate; base attenuate . . . . . (21)

21. Pedicel and flowering calyx glabrous or sparsely pubescent; hairs less than 0.5 mm long, antrorse . . . . 5. *P. longifolia*

21. Pedicel and flowering calyx densely pubescent with divergent hairs that are 1–1.5 mm long, intermixed with antrorse or retrorse hairs that are less than 0.5 mm long . . . . . (22)

22. Leaves oblanceolate with entire margins; pedicel and flowering calyx with both divergent and antrorse hairs . . . . . 17. *P. lanceolata*

22. Leaves ovate to broadly lanceolate with dentate margins; pedicel and flowering calyx with both divergent and retrorse hairs . . . . 18. *P. virginiana*

1. *Physalis carpenteri* Riddell *ex* Rydb.

Perennial, 6–10 dm tall, from a stout rhizome. Stems erect, branching frequently, the branches divergent; pubescent with simple, jointed hairs of varying lengths. Leaf blades ovate to ovate-lanceolate; 5–10 (–14) cm long, 3–6 (–9) cm wide; puberulous; apex acuminate; margins entire or rarely coarsely and irregularly dentate; base truncate to rounded; petiole 1/4–1/2 blade length. Flowers 2 or more in leaf axils. Flowering calyx 4.5–7.5 mm long, sparsely pubescent; lobes 1.5–3.5 mm long, typically unequal; pedicel 5–10 mm long. Corolla pale yellow, with 5 pale brown or green smudges in throat; 8–12 mm long. Anthers yellow, 1.5–2.5 mm long; filament less than 1/2 as wide as anther. Fruiting calyx green, only slightly inflated, 10-angled, base rounded; 1–2 cm long, 1–2 cm in diameter; pedicel 5–15 mm long. Spherical, seed-like bodies interspersed with the seeds. ($n = 12$) Flowering mid-June to early September.

This species is found in moist sand or clay soils, in hardwood and mixed pine-hardwood forests, near rivers, and disturbed habitats such as roadsides and waste areas in the Coastal Plain Province. Specimens were seen from Florida, Louisiana, and Mississippi.

Physalis carpenteri is very different from the other members of the genus in having clustered flowers, apparently due to the presence of a telescoped axillary branch (Waterfall 1958). In a recent infrageneric study based on morphology and chloroplast DNA, Martínez (1999) showed *P. carpenteri* to be part of a monophyletic *Physalis*. One sheet examined notes the species to be an annual, but the large underground portion of the specimens examined appears similar to the rhizomes of perennial taxa. Many specimens include only the upper branches, and despite attempts to re-locate populations documented by herbarium specimens, I have not seen this species in the field.

2. *Physalis alkekengi* L. (Chinese Lantern Plant)

Perennial, 3–9 dm tall, from a stout rhizome. Stems erect, usually unbranched; glabrous or sparsely hairy with simple, short, divergent hairs. Leaf blades broadly ovate; 6–11 cm long, 4–8.5 cm wide; glabrous to sparsely pubescent; apex acute; margins entire or irregularly dentate; base truncate to subcordate; petiole 1/10–2/5 blade length. Flowers solitary in leaf axils. Flowering calyx 4–7 mm long, tomentose with long, simple hairs; lobes 2–3.5 mm long; pedicel 9–13 mm long. Corolla white, without darker spots or smudges in the throat; 10–15 mm long. Anthers yellow, 2.5–3 mm long; filaments less than 1/2 as wide as anthers. Fruiting calyx reddish or bright red, 10-angled, base sunken; 3–5.5 cm long, 2.5–4.5 cm in diameter; pedicel 20–40 mm long. ($n = 12$) Flowering in June.

This species is a native of Europe that is often grown for its ornamental fruiting calyx and then locally spread from cultivation. In my New Hampshire garden, *Physalis alkekengi* spreads aggressively by vegetative means and no viable seeds have been produced. However, habitats mentioned on collection labels were fence rows, thickets, vacant lots, roadsides, and streambanks, more likely indications of reproduction by seed. Only about 12 specimens were seen, mostly from northern states of the region such as Maryland, Tennessee, Virginia, and West Virginia [one specimen from adjacent Pennsylvania].

3. *Physalis philadelphica* Lam. (Tomatillo)

Annual, 1.5–10 dm tall, from a slender taproot. Stems erect, branching, the upper branches divergent; glabrous to sparsely hairy with simple, short, appressed hairs. Leaf blades ovate to ovate-lanceolate; 2–7 cm long, 2–4 cm wide; glabrous or sparsely hairy; apex acuminate; margins dentate to entire; base rounded to attenuate; petiole 1/2 to as long as blade. Flowers solitary in leaf axils. Flowering calyx 5–7 (–10) mm long, sparsely vestite to glabrous; lobes 2–4 mm long; pedicel 3–6 mm long. Corolla yellow, with 5 blue-tinged spots or smudges in throat; 7–15 mm long. Anthers blue, strongly twisted after dehiscence, 3 mm long; filaments about 1/2 as wide as anthers. Fruiting calyx green, nearly filled or often burst by the viscid pale green to purplish or purple-streaked berry, 10-angled, sunken at base; 2–3 cm long, 2–3 cm in diameter; pedicel 3–8 (–11) mm long. ($n = 12$) Flowering all year in areas without frost.

This species has been introduced from the southwest and Mexico. It is cultivated for its fruits, which are commonly used in salsa. The species escapes frequently and becomes established in disturbed sites such as fence rows, edges of cultivated fields, and along roadsides. Only about 10 specimens were seen, mostly from northern states of the region such as Maryland, Tennessee, Virginia, and West Virginia [one specimen from adjacent Illinois].

4. *Physalis angustifolia* Nutt.

Perennial, 1.5–6 dm tall, from a deeply buried rhizome, often also with slender, shallow rhizomes. Stems and lower branches erect or spreading along the ground and ascending; glabrous. Leaf blades narrowly spathulate to linear-lanceolate; 3–10 (–12) cm long, 0.2–1.5 (–2) cm wide; glabrous or with sparse, branched hairs on the margins; apex obtuse to acute; margins entire; base tapering to stem; sessile. Flowers

solitary in leaf axils. Flowering calyx 5–9 (–10) mm long, glabrous except for the margins or, occasionally entire calyx sparsely pubescent with dendroid-stelliform hairs; lobes (1–) 1.5–3.5 mm long; pedicel 11–24 (–32) mm long. Corolla yellow, with 5 ochre to green smudges in throat, the main vein of each corolla lobe often purple to red; (8–) 11–15 (–16) mm long. Anthers yellow, 2.5–3.5 mm long; filaments 1/2 to as wide as anthers. Fruiting calyx typically orange when ripe but drying brown, 10-angled, sunken at base; (1.5–) 2–3 (–4) cm long, 1.5–2.5 cm in diameter; pedicel 15–35 (–42) mm long. ($n = 12$) Flowering all year in areas without frost.

This species is found on beach dunes, edges of pine woods, and disturbed coastal areas in sand in the Gulf Coastal Plain Province. Specimens were seen from Alabama, Florida, Louisiana, and Mississippi.

Physalis angustifolia hybridizes with *P. walteri* in disturbed, sandy habitats of peninsular Florida and populations can be found in the state that exhibit intermediate floral and vegetative characteristics. Waterfall (1958) recognized these intermediates as forms of a broadly defined *P. viscosa* (*P. viscosa* var. *elliottii* f. *elliottii* and f. *glabra*). *Physalis angustifolia* and its relationship to the members of the genus with dendroid-stelliform hairs were examined in detail by Sullivan (1985).

5. *Physalis longifolia* Nutt.

Perennial, 2–6 dm tall, from a stout, deeply buried rhizome. Stems erect, branching frequently on upper portions of plant; glabrous to sparsely hairy with short, simple, antrorse hairs, 0.5 mm or less long. Leaf blades ovate to ovate-lanceolate or broadly lanceolate; 2.5–10 (–13) cm long, 1–6 (–7) cm wide; glabrous or sparsely strigose with short, antrorse hairs; apex acute; margins entire to coarsely dentate with only a few teeth; base truncate to rounded; petiole 1/5–2/5 blade length. Flowers solitary in leaf axils. Flowering calyx (5–) 7–12 (–15) mm long, sparsely strigose with short, antrorse hairs; lobes 3–6 mm long; pedicel 5–20 mm long. Corolla yellow, with 5 purple-brown smudges in throat; 10–20 mm long. Anthers yellow or tinged blue, 2–4 mm long; filaments as wide as or wider than anthers. Fruiting calyx green, 10-angled, rounded or only slightly sunken at base; 2–4 cm long, 1.5–3 cm in diameter; pedicel 15–35 mm long. ($n = 12$) Flowering May through October.

In the past, this species has been aligned with *Physalis virginiana* (Waterfall 1958) and morphological variation has been given taxonomic recognition. More recent assessment has favored the recognition of

P. longifolia as a distinct species. This, as well as the recognition of a morphological and geographically based variant, var. *subglabrata*, is supported by my field observations and survey of herbarium specimens. The typical variety is more common in the central U.S. and has narrower leaves that are slightly more pubescent. Anther color further serves to distinguish the two reliably.

Leaf blades lanceolate; anthers yellow . . . . . 5a. var. *longifolia*
Leaf blades ovate to ovate-lanceolate; anthers tinged blue . . . . . 5b. var. *subglabrata*

5a. var. *longifolia*

Leaf blades 2.5–7.5 cm long, 0.5–2.5 cm wide. Flowering pedicel 5–14 mm long. Corolla 9–13 mm long. This is a variety typically of the prairie region of the central U.S. In the Southeast, specimens can be found in fields, open woods, sandy areas, and disturbed sites, primarily in the Ozark Plateau and Arkansas Valley. Specimens have been seen from Arkansas and Mississippi [also from adjacent Missouri, Oklahoma, and Texas].

5b. var. *subglabrata* (Mack. & Bush) Cronquist

Leaf blades 3.5–10 cm long, 2–6 cm wide. Flowering pedicel 8–18 mm long. Corolla 10–18 mm long. This variety is found in open woods, fields, river bottoms, and disturbed habitats such as roadsides and cultivated sites in all provinces. Specimens have been seen from all states in the region [also from adjacent Illinois, Indiana, Missouri, New Jersey, Ohio, Oklahoma, and Pennsylvania].

Synonym: *Physalis virginiana* var. *subglabrata* (Mack. & Bush) Waterf. (Radford et al. 1968).

6. *Physalis pubescens* L.

Annual, 0.5–8 dm tall, from a slender taproot. Stems erect, branching frequently, the branches divergent; glabrous to villous with simple, jointed, glandular hairs of varying lengths, all shorter than 0.5 mm long. Leaf blades broadly ovate to orbicular; 2.5–8 cm long, 2–7 cm wide; villous with glandular hairs to almost glabrous; apex acute to short-acuminate; margins coarsely dentate with only a few teeth (fewer than 10 per side) or entire; base rounded; petiole from 1/5 to as long as blade. Flowers solitary in leaf axils. Flowering calyx 3–6 mm long, villous to almost glabrous; lobes 1–3.5 mm long; pedicel 3.5–9 mm long. Corolla yellow, with 5 large, dark purple-brown spots in throat; 6–11 mm long.

Anthers blue or rarely only tinged blue, 1–2 mm long; filaments as wide as anthers. Fruiting calyx green, sharply 5-angled, base sunken; 2–3 cm long, 1.5–2.5 cm in diameter; pedicel 6–15 mm long. ($n = 12$) Flowering all year in areas without frost.

This species is found in fields, pastures, hammocks, low woods, edges of swamps, riverbanks, and disturbed habitats such as roadsides and waste ground in all provinces. Specimens have been seen from all states in the region, as well as all adjacent states.

Synonym: *Physalis pubescens* var. *glabra* (Michx.) Waterf., in part (Radford et al. 1968).

In the past, this species has been broadly defined to include *Physalis cordata* and *P. grisea*, and several morpholgical variants have been recognized (e.g., Gleason and Cronquist 1991; Waterfall 1958). More recent taxonomic opinion favors the recognition of *P. cordata* and *P. grisea* as distinct morphological species. *Physalis pubescens*, as treated here, includes both var. *pubescens* and var. *integrifolia* (Dunal) Waterf. without taxonomic recognition of varieties. In my field observations and survey of herbarium specimens, morphological intergradation was seen in all characteristics and no geographic or habitat distinction could be discerned between them. A systematic study focused on the variation in this and related species may provide insight into the nature of the variation observed.

7. *Physalis cordata* Mill.

Annual, 1.5–5 dm tall, from a slender taproot. Stems erect, branching frequently; glabrous or sparsely hairy with simple, appressed hairs that are less than 0.5 mm long. Leaf blades broadly ovate to orbicular; 4.5–8.5 cm long, 3.5–7.5 cm wide; glabrous except for sparse hairs on veins; apex acuminate; margins coarsely dentate with 10 or more teeth per side; base rounded to truncate or cordate; petiole 2/3 to as long as blade. Flowers solitary in leaf axils. Flowering calyx 3.5–6.5 mm long, glabrous or very sparsely hairy; lobes 2–4.5 mm long; pedicel (4.5–) 6–11 mm long. Corolla yellow, with 5 large purple-brown spots in throat; 6.5–9.5 mm long. Anthers blue or blue-tinged, 1.5–2.5 mm long; filaments as wide as anthers. Fruiting calyx green, glabrous, sharply 5-angled, sunken at base; (2.5–) 3–4 cm long, 2–3 cm in diameter; pedicel (10–) 15–35 mm long. Flowering July through October.

This species is found primarily in sandy soils, along rivers, in pine woods, and in disturbed habitats such as yards and fields, chiefly in the Coastal Plain Province but also from the Piedmont in Tennessee and Mountain Provinces in Arkansas. Specimens have been seen from

Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, and Tennessee [also from adjacent Oklahoma and Texas].

Synonym: *Physalis pubescens* var. *glabra* (Michx.) Waterf., in part (Radford et al. 1968).

Physalis cordata is quite distinctive, morphologically. It can be distinguished from *P. pubescens*, with which it has been considered conspecific, by the large, coarse teeth on its leaf margins and its long fruiting pedicels. Any systematic study of *P. pubescens* should include *P. cordata*, in order to better understand the relationship between these two taxa.

8. *Physalis missouriensis* Mack. & Bush

Annual, 1.5–5.5 dm tall, from a slender taproot. Stems erect, branching frequently; sparsely to densely pubescent with simple, jointed, glandular and non-glandular hairs that are less than 0.5 mm long. Leaf blades broadly ovate to orbicular; 2.5–5.5 cm long, 1.5–5 cm wide; sparsely glandular-pubescent; apex acute; margins irregularly and shallowly dentate; base rounded or sometimes truncate; petiole 2/5 to as long as blade. Flowers solitary in leaf axils. Flowering calyx 2.5–4 mm long, densely glandular-pubescent; lobes 1–2 mm long; pedicel 4–7 mm long. Corolla yellow, without darker spots or smudges in throat; 5–7 mm long. Anthers yellow, 1–1.5 mm long; filaments less than 1/2 as wide as anthers. Fruiting calyx green, densely glandular-hairy, 10-angled, rounded or only very slightly sunken at base; 1–2 cm long, 1–2 cm in diameter; pedicel 5–10 mm long. Flowering June through August.

This species is found on rocky bluffs, dolomite ledges, cliffs, and wooded slopes on the Ozark Plateau. Specimens have been seen from Arkansas [also from adjacent Missouri and Oklahoma].

9. *Physalis angulata* L.

Annual, 1–20 dm tall, from a large taproot. Stems erect, branching frequently; glabrous or sparsely hairy with simple, jointed hairs that are 0.5 mm or less long. Leaf blades elliptic to linear-lanceolate; 3–10 (–14) cm long, 1–8 cm wide; glabrous to sparsely hairy; apex acuminate; margins deeply and coarsely irregularly dentate with acuminate teeth; base rounded to attenuate; petiole 1/3–2/3 blade length. Flowers solitary in leaf axils. Flowering calyx 3–5 mm long; sparsely hairy or glabrous except for margins; lobes 1–3 mm long; pedicel 7–17 (–22) mm long. Corolla yellow, without spots or smudges or only rarely tinged purple in throat; 6–10 mm long. Anthers blue or blue-tinged, 1–3 mm long;

filaments less than 1/2 as wide as anthers. Fruiting calyx green, 10-angled, only slightly sunken at base; 2–4 cm long, 1.5–2.5 cm in diameter; pedicel 15–30 mm long. (n = 12, 24) Flowering all year in areas without frost.

This species is found in hardwood and pine woods, woodland borders, sandhills, stream margins, edges of marshy areas, fields, pastures, and waste places, chiefly in the Coastal Plain and Piedmont Provinces. Specimens have been seen from Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, and Virginia [also from adjacent Illinois, Missouri, Oklahoma, and Texas].

Some plants in southern Florida have linear to lanceolate, sinuate leaf blades and very small flowers (corollas 4–5 mm long). These have been given taxonomic recognition in the past as *Physalis angulata* var. *pendula* Rydb. However, examination of over 1000 herbarium sheets revealed an intergradation of morphology between var. *angulata* and var. *pendula*, and no geographic or habitat distinction between the two. Another species, *P. acutifolia* (Miers) Sandwith, so closely resembles the narrow-leaved populations of *P. angulata* in vegetative characters that they could not be distinguished, even in the field. When in flower, *P. acutifolia* is distinctive in having flowering pedicels 15–40 mm long, a widely flaring corolla limb, and a slightly smaller fruiting calyx that is nearly filled by the mature berry. *Physalis acutifolia* is a species of the southwestern U.S., but specimens were seen from Bolivar County, Mississippi in an area that had been under cultivation previously.

10. *Physalis pumila* Nutt.

Perennial, 1.5–4 dm tall, from a stout deeply buried rhizome. Stems erect, branching infrequently at upper nodes, the branches ascending; hispid with jointed, simple and/or 2–3 branched hairs that are 0.5–2 mm long. Leaf blades ovate to ovate-lanceolate; 3–8 (–10) cm long, 2–5 cm wide; hispid; apex acute; margins entire to undulate, rarely sinuate-dentate; base attenuate; petiole 1/10–2/5 blade length. Flowers solitary in leaf axils. Flowering calyx 6–12 mm long, hispid; lobes (2.5–) 3–5 (–6) mm long; pedicel (7–) 14–30 mm long. Corolla yellow, tinged pale brown or green in throat but without distinct spots or smudges; 11–16 mm long. Anthers yellow, 2–3 mm long; filaments as wide as anthers. Fruiting calyx green, 10-angled, sunken at base; 2.5–3.5 (–4) cm long, 1.5–3 cm in diameter; pedicel 25–55 mm long. (n = 12) Flowering early March through September.

This species can be found in dry, rocky soil in prairies, fields, and disturbed habitats. A species chiefly of prairies in the central U.S. In the Southeast specimens have been seen from the Gulf Coastal Plain and Mountain Provinces of western Arkansas and Louisiana [also from adjacent Missouri, Oklahoma, and Texas].

11. *Physalis mollis* Nutt.

Perennial, 1.5–5 dm tall, from a stout, deeply buried rhizome, often also with slender, shallow rhizomes. Stems erect, branching occasionally, the branches ascending; tomentose with dendroid-stelliform hairs that are less than 1 mm long and obscuring the plant surface, occasionally also with 2–4 mm long jointed, dendroid-stelliform or unbranched hairs at lower nodes. Leaf blades ovate; 2.5–7 cm long, 1.5–6 (–7) cm wide; tomentose; apex acute; margins coarsely dentate or irregular to almost entire; base truncate; petiole 1/3–4/5 blade length. Flowers solitary in leaf axils. Flowering calyx 6–10 (–12) mm long, tomentose with short, dendroid-stelliform hairs, occasionally also with long, unbranched, jointed hairs; lobes 2.5–5.5 mm long; pedicel 10–25 (–35) mm long. Corolla yellow, with 5 pale brown to dark brown smudges in throat; 9.5–15 (–17) mm long. Anthers yellow or rarely with a blue or purple tinge, 3–4 mm long; filaments about 1/2 as wide as anthers. Fruiting calyx green, 10-angled, sunken at base; 2.5–4 (–5) cm long, 1.5–3 cm in diameter; pedicel 20–40 (–52) mm long. ($n = 12$) Flowering early March through October.

This species can be found in sandy soil in prairies, along roadsides, and disturbed habitats. Coastal Plain and Mountain Provinces. Specimens have been seen from Arkansas and Louisiana [also from adjacent Oklahoma and Texas]. Relationships among the *Physalis* species with dendroid-stelliform hairs were examined in detail by Sullivan (1985).

12. *Physalis cinerascens* (Dunal) Hitchc.

Perennial, 0.5–5 dm tall, from a large, deeply buried rhizome. Stems and lower branches erect or spreading along the ground and ascending; sparsely to moderately densely pubescent with dendroid-stelliform hairs that are 1 mm or less long. Leaf blades ovate to spathulate; 1.5–8 (–9) cm long, 1–6 (–8) cm wide; sparsely to moderately densely pubescent; apex acute or obtuse; margins coarsely dentate, sinuate, undulate, or entire; base truncate to attenuate; petiole 1/5 to as long as blade. Flowers solitary in leaf axils. Flowering calyx (3.5–) 5–9 mm long, pubescent; lobes 1.5–4 mm long; pedicel 10–33 mm long. Corolla yellow, with 5

dark purple-black spots in throat, these sometimes bisected by the yellow main veins of the corolla; (8–) 9–16 mm long. Anthers yellow or rarely with a purple tinge, 2–5 mm long; filaments 1/2 to as wide as anthers. Fruiting calyx green, 10-angled, sunken at base; 1.5–3.5 (–4.5) cm long, 1–3.5 cm in diameter; pedicel 15–60 mm long. (n = 12) Flowering all year in areas without frost.

Leaves ovate; leaf base truncate to slightly attenuate; leaf margins dentate, sinuate, or entire; corolla limb reflexed when fully open . . . . . 12a. var. *cinerascens*

Leaves spathulate; leaf base attenuate; leaf margins entire; corolla limb not reflexed when fully open . . . . 12b. var. *spathulaefolia*

12a. var. *cinerascens*

Fruiting calyx 1.5–3 cm long, 1–2 cm in diameter, fruiting pedicel 15–60 mm long. This variety can be found in prairies, fields, roadsides, and disturbed habitats. Chiefly Coastal Plain. Specimens have been seen from Arkansas and Louisiana [also from adjacent Oklahoma and Texas]. This is a species primarily of the prairies and mountains in the south-central U.S., but occasionally it is found elsewhere in the Southeast. The pollination biology of *Physalis cinerascens* var. *cinerascens* has been described by Sullivan (1984, as *P. viscosa* var. *cinerascens*). The relationship between the two varieties of *P. cinerascens* was examined in detail by Sullivan (1985).

12b. var. *spathulaefolia* (Torr.) J.R. Sullivan

Fruiting calyx 2.5–4.5 cm long, (1.5–) 2–3.5 cm in diameter, fruiting pedicel 25–60 mm long. This variety is found on Gulf dunes and disturbed habitats near the Gulf Coast in sand. Specimens have been seen from Louisiana [also from adjacent Texas]. In the past, this taxon was considered to be more closely related to *Physalis walteri* (as varieties of *P. viscosa* subsp. *maritima*; Waterfall 1958). Both are taxa of coastal sand dunes and have similar vegetative morphology, which is eye-catching when working primarily with herbarium specimens. Relationships among the taxa with dendroid-stelliform hairs were examined in detail by Sullivan (1985).

13. *Physalis walteri* Nutt.

Perennial, 0.5–4 dm tall, from a stout and usually deeply buried rhizome. Stems and lower branches erect or spreading along the ground and ascending; sparsely to moderately densely covered with dendroid-stelliform hairs that are 1 mm or less long. Leaf blades elliptic or ovate

to ovate-lanceolate; (2.5–) 3.5–11 (–13) cm long, 1.5–5 (–7) cm wide; sparsely to moderately densely pubescent; apex obtuse or acute; margins entire or rarely undulate; base rounded to attenuate; petiole 1/6–1/2 blade length. Flowers solitary in leaf axils. Flowering calyx (5–) 6–9 (–11) mm long, pubescent; lobes 1.5–4 (–5) mm long; pedicel 9–25 (–35) mm long. Corolla yellow, with 5 dark brown to pale brown, ochre, or green spots or smudges in throat, the main veins of the corolla lobes sometimes purple or red; (9–) 11–15 (–18) mm long. Anthers yellow or infrequently tinged purple, 2.5–3.5 mm long; filaments as wide as anthers. Fruiting calyx green, 10-angled, sunken at base; 2–3.5 cm long, 1.5–2.5 cm in diameter; pedicel 15–35 (–45) mm long. ($n = 12$) Flowering all year in areas without frost.

This species is found on beach dunes and in disturbed areas in sand. Coastal Plain. Specimens have been seen from Alabama, Florida, Georgia, Mississippi, North Carolina, South Carolina, and Virginia.

Synonym: *Physalis viscosa* subsp. *maritima* (M.A. Curtis) Waterf. (Radford et al. 1968).

Physalis walteri hybridizes with *P. angustifolia* in disturbed, sandy habitats of peninsular Florida and populations can be found in the state that exhibit intermediate floral and vegetative characteristics. Waterfall (1958) recognized these intermediates as forms of a broadly defined *P. viscosa* (*P. viscosa* var. *elliottii* f. *elliottii* and f. *glabra*). Relationships among the members of the genus with dendroid-stelliform hairs were examined in detail by Sullivan (1985).

14. *Physalis grisea* (Waterf.) M. Martínez

Annual, 3–6 dm tall, from a large taproot. Stems erect, branching frequently, the branches spreading; villous with simple, jointed hairs that are 0.5–1 mm long. Leaf blades broadly ovate; 3.5–11 cm long, 2.5–10 cm wide; gray-green, drying orange or with orange patches; pubescence of short, simple hairs that are ca. 0.5 mm long intermixed with stalked glands that are much shorter than 0.5 mm long and sessile glands; apex acute; margins coarsely dentate; base broadly rounded to slightly cordate; petiole 2/5–4/5 blade length. Flowers solitary in leaf axils. Flowering calyx 3–5 mm long, short-pubescent; lobes 1.5–2.5 mm long; pedicel 4–6 mm long. Corolla yellow, with 5 large, dark purple-brown spots in throat; 5–8 mm long. Anthers blue or tinged blue, 1–2 mm long; filaments 1/2 as wide as anthers. Fruiting calyx green, sharply 5-angled, sunken at base; 2–3.5 cm long, 1.5–2.5 cm in diameter; pedicel 5–12 mm long. ($n = 12$) Flowering June through October.

This species is found in open areas such as meadows, pastures, disturbed woodlands and river bottoms, and cultivated sites. Chiefly Mountain and Piedmont Provinces. Specimens have been seen primarily from North Carolina, South Carolina, Tennessee, and West Virginia, but sporadically elsewhere in the Southeast [also from adjacent Ohio and Pennsylvania].

Synonym: *Physalis pubescens* var. *grisea* Waterf. (Gleason and Cronquist 1991; Radford et al. 1968).

Most specimens of this species were annotated by me as *Physalis pruinosa* L., based on synonymy given in Waterfall (1958). The application of that name has since been clarified by Martínez (1993), who determined that the correct name for our plants is *P. grisea*. *Physalis grisea* can be distinguished from *P. pubescens*, with which it has been considered conspecific, by the often larger leaves that have a distinctive gray-green color and exhibit orange patches on drying. Closer examination of the foliage of *P. grisea* reveals sessile or short-stalked glands as opposed to the glandular hairs of *P. pubescens*. Any systematic study of *P. pubescens* should include *P. grisea*, in order to better understand the relationship between these two taxa.

15. *Physalis heterophylla* Nees

Perennial, 1.5–10 dm tall, from a stout, deeply buried rhizome. Stems erect to decumbent, branching frequently, branches spreading along the ground and ascending; villous with simple, jointed, divergent hairs that are 1–2 mm long, often also with shorter, glandular hairs. Leaf blades broadly ovate to sub-orbicular; (3–) 4–11 (–13) cm long, 3–9 (–10) cm wide; villous and often glandular; apex acute; margins deeply and irregularly dentate to almost entire; base truncate to slightly cordate; petiole 1/3–2/3 blade length. Flowers solitary in leaf axils. Flowering calyx 6–12 mm long, villous and often glandular; lobes 3–6 mm long; pedicel 9–15 (–20) mm long. Corolla yellow, with 5 large purple-brown smudges in throat; 10–17 mm long. Anthers yellow or infrequently tinged blue, 2.5–4.5 mm long; filaments as wide as anthers and usually conspicuously clavate at apex. Fruiting calyx green, 10-angled, sunken at base; 2.5–4 cm long, 1.5–3 cm in diameter; pedicel 20–30 mm long. ($n = 12$) Flowering May through September.

This species is found in open hardwood forests, edges of pine woods, fields, roadsides, and disturbed sites, often in shade. This is a widespread species, and is found in all provinces. Specimens have been seen from all states in the region, as well as all adjacent states.

There is some morphological variation in this species, which in the past has been recognized taxonomically (Waterfall 1958). Varieties are not recognized here, since I found morphological intergradation between them and none could be identified reliably. Further study may provide insight into the nature of this variation. In 1975 Hinton reported the occurrence in North Carolina of a population representing a natural hybridization event between *Physalis heterophylla* and *P. virginiana*.

The cultivated *Physalis peruviana* L. (Cape Gooseberry) is similar to *P. heterophylla*. No specimens of this species were seen except for those from gardens, however. *Physalis peruviana* is an erect plant that is not glandular, the pedicels are shorter than those of *P. heterophylla* (6–8 mm in flower; 13–15 mm in fruit), the anthers are blue or blue-tinged, and the filaments are 1/2 as wide as the anthers.

16. *Physalis arenicola* Kearney

Perennial, 0.5–3 dm tall, from a slender, deeply buried rhizome, typically also with slender, shallow rhizomes. Stems erect, few-branched; glabrous to villous with simple, antrorse hairs that are less than 1 mm long, sometimes interspersed with 1–2 mm long, simple, jointed hairs, sometimes viscid. Leaf blades ovate to sub-orbicular; 1.5–6 (–6.5) cm long, 1–5 cm wide; villous with short, glandular and long, jointed hairs or rarely almost glabrous; apex acute; margins entire to coarsely and irregularly dentate with few teeth; base truncate to cordate; petiole 1/4–2/3 blade length. Flowers solitary in leaf axils. Flowering calyx 6–12 mm long, villous; lobes 2–5 mm long; pedicel (8–) 11–17 (–45) mm long. Corolla yellow, with 5 pale reddish-brown smudges in throat or without smudges; 10–17 mm long. Anthers yellow, 2.5–4 mm long; filaments 1/2 to as wide as anthers. Fruiting calyx green, 10-angled, slightly sunken at base; 2–3.5 cm long, 1.5–2.5 cm in diameter; pedicel 15–30 (–35) mm long. ($n = 12$) Flowering all year in areas without frost.

This species is found in sand or sandy soil in woods, hammocks, fields, pastures, and along roadsides. Coastal Plain. Specimens have been seen from Alabama, Florida, and Georgia.

Pressed specimens are sometimes difficult to distinguish from *Physalis heterophylla*. *Physalis heterophylla* is a widespread and morphologically variable species. The presence of slender, cord-like, shallow rhizomes and typically very short pubescence are distinctive for *P. arenicola*.

17. *Physalis lanceolata* Michx.

Perennial, 2–4 dm tall, from a large, stout rhizome. Stems decumbent, branching infrequently; sparsely pubescent with simple,

antrorse hairs that are 0.5 mm or less long, or with simple, jointed, divergent hairs that are 1–1.5 mm long. Leaf blades oblanceolate; 4–10 cm long, 2–6 cm wide; pubescent with short, appressed and long, divergent hairs; apex acute; margins entire to slightly undulate; base attenuate; petiole 1/25–1/3 blade length. Flowers solitary in leaf axils. Flowering calyx 6–10 mm long, hispid with long, jointed hairs; lobes 2–5 mm long; pedicel 10–20 mm long. Corolla yellow, with 5 pale brown smudges in throat; 10–15 mm long. Anthers yellow, 2.5–3.5 mm long; filaments 1/2 as wide as anthers. Fruiting calyx green, 10-angled, scarcely sunken at base; 2–3.5 cm long, 1.5–3 cm in diameter; pedicel 10–30 mm long. (n = 12) Flowering April through September.

This species is found in sandhills, primarily in the Atlantic Coastal Plain, but also in some Piedmont counties in North Carolina. Specimens have been seen from Georgia, North Carolina, and South Carolina.

Southeastern U.S. plants ascribed to this species were considered by Waterfall (1958) to be hybrids between *Physalis heterophylla* and *P. virginiana*, but have since been shown to be a distinct species (Hinton 1970).

18. *Physalis virginiana* Mill.

Perennial, 1–4 dm tall, from a stout rhizome. Stems erect, branching infrequently; hispid with jointed, simple, divergent hairs that are ca. 1 mm long, and retrorse hairs that are 0.5 mm or less long. Leaf blades ovate to broadly lanceolate; 2–7 (–9) cm long, 1–5 (–6) cm wide; pubescent with long, jointed and short, retrorse hairs; apex acute; margins coarsely to shallowly dentate or entire; base truncate to obtuse; petiole 1/5–1/2 blade length. Flowers solitary in leaf axils. Flowering calyx 6–12 (–14) mm long, hispid with long, jointed and short, retrorse hairs; lobes 3–6 mm long; pedicel (6–) 9–19 (–27) mm long. Corolla yellow, with 5 dark purple-brown smudges in throat; 10–17 (–20) mm long. Anthers yellow or sometimes tinged blue, 2–3 mm long; filaments as wide as or wider than anthers. Fruiting calyx green, 10-angled, base sunken; 2–4 cm long, 1.5–3 cm in diameter; pedicel 15–30 mm long. (n = 12) Flowering April through October.

This species is found in prairies, fields, thickets, open woods, and disturbed habitats such as roadsides, cultivated ground, waste places, and along railroads. This is a species primarily of the Midwest and central plains states, but is found sporadically in the Southeast. Specimens have been seen from all states in the region, as well as all adjacent states.

In the past, *Physalis virginiana* has been treated in a broader sense, including *P. longifolia* (Waterfall 1958), and morphological variation has been given taxonomic recognition. More recent assessment has favored the recognition of *P. longifolia* as a distinct species. In 1975 Hinton reported the occurrence in North Carolina of a population representing a natural hybridization event between *P. virginiana* and *P. heterophylla*.

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FLORISTICS AND DISTRIBUTION OF VERNAL POOLS ON THE COLUMBIA PLATEAU OF EASTERN WASHINGTON

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ABSTRACT. Vernal pools are common on the Columbia Plateau of eastern Washington, where they occur on basalt bedrock within the channels scoured by the Pleistocene Missoula Floods. This is the first extensive floristic survey of these pools. Eighty-five percent of the 283 plant taxa are native, and the majority of these are annual. The Washington vernal pools have strong floristic affinities with their counterparts in California; 34% of the native species and 65% of genera in the Columbia Plateau pools also occur in California vernal pools. The remainder include numerous regional and locally endemic taxa. The total native flora is two-thirds that of the California vernal pools, but the average per-pool taxon richness in Washington is greater.

Key Words: vernal pools, Columbia Plateau, Washington, floristics

Vernal pools have long been recognized for their rich and unique biota (Jain and Moyle 1984; Purer 1939; Witham et al. 1998; Zedler 1987). These closed-basin non-wooded habitats containing standing water accumulated from precipitation during the cool season and fully desiccated in summer. They have been well documented within the California Floristic Province, which encompasses the area from southwestern Oregon to Baja California del Norte and inland to the Sierra Nevada (Hickman 1993). However, their existence elsewhere in western North America has been largely overlooked. A large number of seasonal and permanent wetlands occur in the Columbia Plateau of eastern Washington (Figure 1). Many of these wetlands are vernal pools that share abiotic features as well as plant and animal taxa with their Californian counterparts.

There are no published floristic surveys of the vernal pools in eastern Washington. One ecological study examined the relationships between soil and plant distributions around a set of pools in Adams County (Crowe et al. 1994) and another examined the ecology of non-native plants in the same set of pools (Brown 2001). Our investigation was

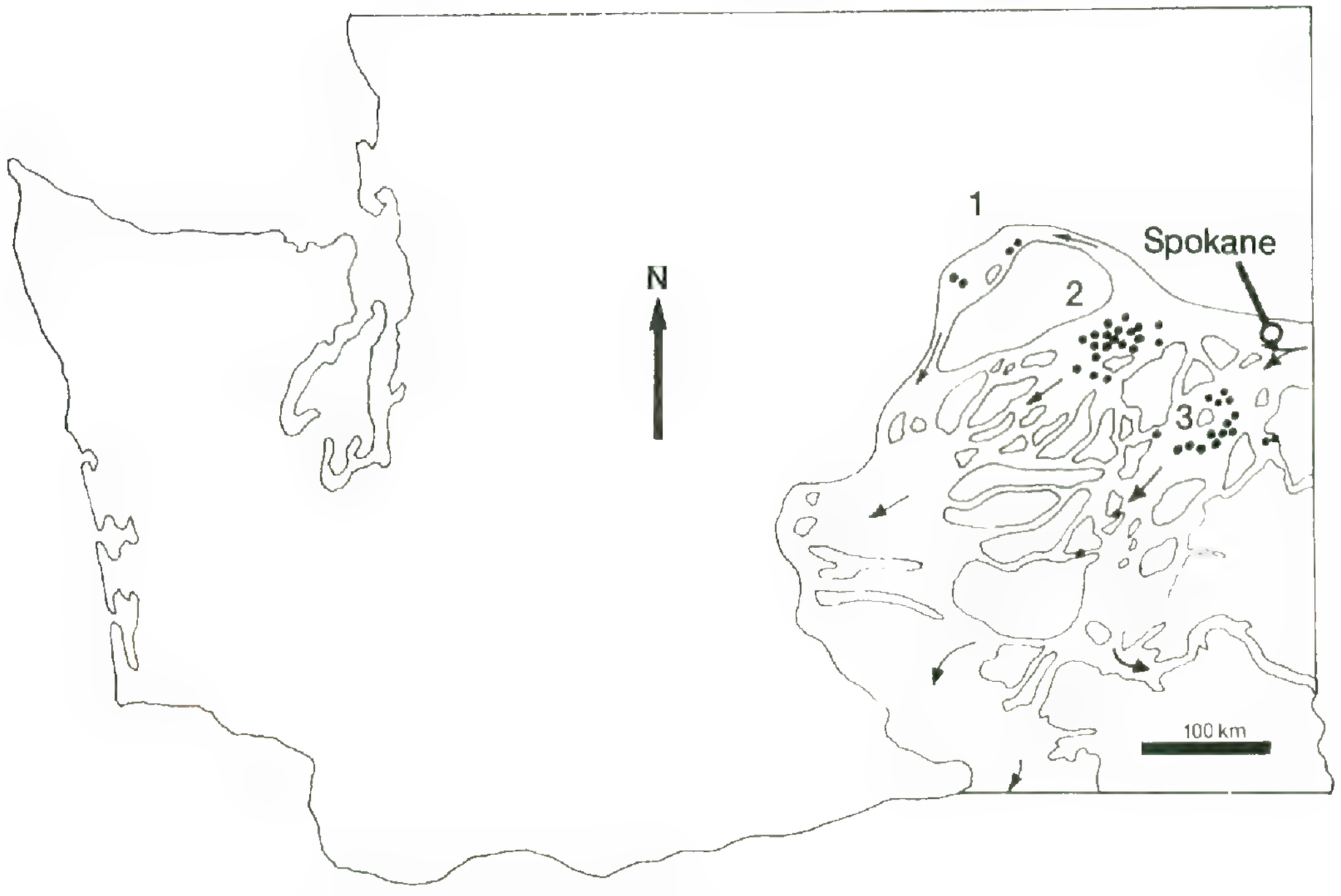

Figure 1. Map of Washington State, showing channels of the Missoula Flood events and study sites. Arrows indicate direction of water flow during floods. Polygons within the flood area indicate upland sites of loess soil that escaped the scouring of the floods. Dots indicate locations of vernal pools and vernal pool complexes studied. Numbers refer to the three main groupings of flood channels on the Columbia Plateau.

initiated to provide basic floristic information on this little-studied region. Specifically, we sought to: (1) determine the geographical extent of vernal pools in the Columbia Plateau of Washington, (2) generate lists of vascular plants associated with the pools, (3) compare their floristic composition with the vernal pools of California, (4) identify taxa that distinguish the Columbia Plateau vernal pools from those of other vernal pool regions, and (5) bring the high ecological value of these vernal pools to the attention of the public and scientific community.

Study area. The Columbia Plateau is a landscape of Miocene flood-basalts overlain by loess, sand, and gravel. A series of immense Late Glacial flood events, known as the Missoula Floods (ca. 15,000 to 12,000 YBP) scoured away loess hills in broad channels, leaving bedrock exposed in a region referred to as the Channeled Scablands (Bretz 1969). There are three main groupings of Missoula Flood channels (Figure 1). The westernmost occur in and around the Grand Coulee; a central group occurs in central Lincoln and Adams Counties; and the eastern channels extend from near Spokane southwestward into southeast Lincoln and

eastern Adams Counties. These channels contain a major concentration of wetlands that occur in shallow basins perched on the basalt bedrock, which is effectively impervious to groundwater movement. Surface drainage is limited to small creeks and intermittent streams.

Precipitation on the plateau is of a Mediterranean pattern, with a winter maximum/summer minimum. Evapotranspiration differs greatly between the cold, humid winters and the hot, arid, nearly cloudless summers. Total precipitation ranges from an average of 23 cm at Coulee City in the west to 36 cm at Spokane in the east (United States Department of Commerce 1973). In the first year of our study, winter precipitation (November–April, 1996–97) averaged 42% above normal, with below-normal temperatures. The second year was significantly warmer and drier, with winter precipitation averaging only 83% of normal across the study area. Water levels and duration of flooding in the pools contrasted greatly between the two years.

MATERIALS AND METHODS

Satellite photographs and ground searches were the primary means used to identify seasonal wetlands in the Scablands. We distinguished California-type vernal pools from other seasonal basin wetlands in the study area based on three criteria: (1) annuals dominant and woody component minimal, (2) lack of surface salt deposits, and (3) presence of taxa characteristic of vernal pools in California, including *Plagiobothrys* sect. *Allocarya*, *Psilocarphus* spp., and *Navarretia leucocephala* subspp. As an additional aid in finding study sites, we sought location information from herbarium specimens of characteristic vernal pool taxa in regional herbaria at Washington State University, Pullman and University of Washington, Seattle (WS and WTU, respectively). However, there were very few collections of these plants from the Columbia Plateau, and most lacked precise location information.

All vascular plant taxa were recorded for 242 vernal pools from April–July, 1997 in Spokane, Adams, Lincoln, Grant, and Okanogan Counties. In 1998, a total of 110 more pools were surveyed, mostly in the Swanson Lakes Wildlife Management Area. We visually estimated pool area and depth. Taxa were recorded as present within vernal pools if we observed them at or below the obvious high-water mark of the current season. Voucher specimens of taxonomically questionable or rare taxa were deposited in WTU and WS. Nomenclature is mostly from Hickman (1993) and generic placement is largely based on APG classification (Angiosperm Phylogeny Group 1998).

Water levels were extremely high in 1997, resulting in the inundation of some adjacent uplands that contain dryland taxa not normally found in vernal pools. Subsequent death of large sagebrush in some of these flooded areas confirmed that water levels had been abnormally high. This inundation frequently resulted in mixing of amphibious vernal pool taxa with those of the surrounding upland communities. Since we sought to characterize the flora typical of pools during normal seasonal inundation, we identified a "core flora" that excluded taxa not well suited to the vernal pool environment. The excluded taxa are not persistent and are unable to withstand the flood or drought stage of vernal pool hydrology.

RESULTS

Vernal pool habitats. California-type vernal pools occur in Adams, Douglas, Grant, Lincoln, Okanogan, and Spokane Counties, where they are all limited to the flat, impervious basalt bedrock exposed by the Missoula Floods. The pools are concentrated in three distinct regions delineated by the Missoula Flood channels. The greatest concentration occurs in the central channel, in and around the Swanson Lakes Wildlife Management Area, which includes some of the least disturbed lands in the Scablands. Vernal pool densities exceed 200 per square-mile section (2.6 km^2) in some areas. The flood channels are separated from each other by expanses of hilly loess uplands averaging approximately 20–30 km wide. No vernal pools occur on these intervening loess hills.

The vernal pools examined in Washington were typically small and shallow. They ranged in area from 3–4608 m^2 with an average of 1592 m^2. Mean minimum depth was 0.47 m. Pools in the eastern channels were smaller (mean and SE = 123 ± 59 m^2) than pools in the west (635 ± 169 m^2; $p = 0.04$) and central channels (2263 ± 488 m^2).

Most of the Columbia Plateau vernal pools lie within a shrub-steppe mosaic composed of sagebrush (*Artemisia* spp.) and various codominant grasses and forbs. In northern and eastern portions of the plateau, they are scattered in open *Pinus ponderosa* stands. Pools in the central and western flood channels are mostly surrounded by shrub-steppe/grassland mosaic. Although many sites are only moderately disturbed, with minimal cover of non-natives, perhaps half of the pools are surrounded by communities significantly altered by non-native taxa such as *Apera interrupta*, *Bromus* sect. *Eubromus*, *Hypericum perforatum*, *Lactuca serriola*, *Poa bulbosa*, *Sisymbrium altissimum*, and *Taeniatherum caput-medusae*.

In 1997, most vernal pools began to dry at the end of May, though very large pools retained standing water through June. In contrast, in

1998, nearly all vernal pools were fully desiccated by the middle of April. We found that small pools were the first to fill with the onset of autumn rains, which occurred in late November in 1997. Large pools did not fill until midwinter, when rainwater and snow melt accumulated during warm Pacific storms. Even in the 1998 drought, medium and large pools held standing water continuously from first flooding until mid-April.

Soils of the vernal pools are grayish silty clays formed in part from volcanic ash. Nitrogen fixation in inorganic vernal pool soils may be primarily from abundant *Nostoc* colonies. Other sources of fixed nitrogen (i.e., Cyanolichens and legumes) are not abundant in vernal pool basins on the Columbia Plateau. Organic matter is minimal, but we observed significant accumulations of organic matter in some east-channel pools where mosses and thatch-forming taxa such as *Carex athrostachya* and *Senecio hydrophiloides* were more abundant.

Most vernal pools form on large expanses of exposed clay with little surface cover. This is particularly apparent post-desiccation, after plant senescence. Cobble-sized basalt rocks are common in many basins, sometimes providing complete cover throughout. Algal mats sometimes form dense cover, typically around *Eleocharis macrostachya* stands and in pools adjacent to roadways. Litter cover is typically minimal, except on margins, among *E. macrostachya* and in pools having abundant thatch-forming non-natives like *Bromus hordaceus*, *Cirsium arvense*, *Elytrigia repens*, *Lactuca serriola*, and *Taeniatherum caput-medusae*.

Moss cover is typically limited to marginal areas, where *Bryum algovicum*, *Ceratodon purpureus*, *Funaria hygrometrica*, *Physcomitrium kellermanii*, *P. pygmaeum*, *P. pyriforme*, and *Tortula bistratosa* sometimes form a distinct band. In the eastern Missoula Flood channel, *Cratoneuron commutatum* and *C. filicinum* sometimes provide dense cover across pool basins. *Orthotrichum rivulorum* is locally common on basalt cobbles in the eastern channel. Liverwort diversity is limited to pool margins, where blooms of *Riccia beyrichiana*, *R. cavernosa*, *Ricciocarpos natans*, *Fossombronia* sp., *Sphaerocarpos mitchellii*, and *S. texanus* form. Of lichens, *Dermatocarpon meiophyllizum*, *D. miniatum*, *Leptogium californicum*, *L. lichenoides*, *L. subaridum*, and *Aspicillia aff. contorta* are the only common taxa known to us in pool basins, where they grow on cobbles.

All vernal pools we surveyed are bordered by or are in the near vicinity of Mima mounds, which on the Columbia Plateau are round knolls of loamy soil about 1 m high, often perched on bare basalt. The lowest slopes of the mounds are often below annual high water mark and

Table 1. Numerical analysis of the Columbia Plateau vernal pool flora. The core flora omits any taxa that are uncommon, nonpersistent, and appear intolerant of the vernal pool flood or desiccation period.

	Number of Species				
Plant Type	All Taxa	Native Taxa	Core Natives	Non-native Taxa	Core Non-natives
Annual	157	132	111	25	16
Perennial	112	95	61	17	12
Woody	14	14	3	0	0
TOTAL	283	241	175	42	28

vernal pool species that prefer marginal areas typically form a distinct band of dense cover at mound base.

Vascular plant flora. Eighty-five percent of the 283 vascular plant taxa associated with the vernal pools were native (Table 1; Appendix). The 203 species that constituted the core vernal pool flora—taxa well adapted to the pool environment—included 28 non-natives and 175 natives. The core native flora was predominantly annual (63%), with abundant graminoids (45 taxa; 36 Poaceae) and composites (40 Asteraceae). Of the 14 woody taxa, all were native and only 3 were members of the core flora (*Eriogonum compositum*, *E. heracleoides*, and *Talinum spinescens*). The remaining woody taxa found were poorly adapted to flooding and were typically flood-killed.

The Columbia Plateau vernal pools have many floristic similarities to their California counterparts (Table 2). Thirty-four percent of the native taxa and 65% of the genera we found also occur in a comprehensive listing of California vernal pool taxa (Keeler-Wolf et al. 1998). The first author has recorded from Butte and Modoc Counties, California another seven native taxa shared between the two regions' vernal pools (*Carex athrostachya*, *Castilleja tenuis*, *Heterocodon rariflorum*, *Juncus hemiendytus* var. *hemiendytus*, *Myosurus clavicaulis*, and *Trifolium*

Table 2. Comparison of vascular plant taxon richness of vernal pools in California and on the Columbia Plateau of Washington. California figures are from the California Department of Fish and Game website (Keeler-Wolf et al. 1998).

	Number of Species		
Taxon Category	California	Columbia Plateau	Shared
Native genera	138	116	75
Native total taxa	367	224	77
Non-native total taxa	67	28	10

microcephalum). Ten of the 28 core non-native taxa are shared with the California vernal pools: *Amaranthus albus*, *Bromus hordaceus*, *Capsella bursa-pastoris*, *Convolvulus arvensis*, *Holosteum umbellatum*, *Polypogon monspeliensis*, *Rumex crispus*, *Spergularia bocconii*, *S. rubra*, and *Taeniatherum caput-medusae*.

Twenty-three of the most abundant and widespread taxa of the Columbia Plateau vernal pools have not been reported from vernal pools in California (Keeler-Wolf et al. 1998). Among these are *Achillea millefolium*, *Amsinckia* spp., *Artemisia ludoviciana* subsp. *ludoviciana*, *Camassia quamash* subsp. *quamash*, *Camissonia andina*, *Critesion jubatum*, *Cyperus squarrosus*, *Danthonia unispicata*, *Geranium bicknellii*, *Lagophylla ramosissima*, *Leymus cinereus*, *Lomatium bicolor* subsp. *leptocarpum*, *L. grayi*, *Madia* spp., *Microsteris gracilis*, *Montia dichotoma*, *M. linearis*, *Perideridia montana*, *Plantago patagonica*, *Poa scabrella*, *Sanguisorba occidentalis*, *Senecio hydrophiloides*, and *Trifolium cyathiferum*. Fifteen common and widespread non-natives have also not been reported from the California vernal pools, such as *Cirsium arvense*, *Elytrigia repens*, *Lactuca serriola*, *Poa compressa*, and *Sisymbrium altissimum*. Several core natives have not been found in California at all, including *Allium columbianum*, *A. geyeri* var. *geyeri*, *Camissonia hilgardii*, *Centaurium curvistamineum*, *Cirsium brevifolium*, *Clarkia pulchella*, *Delphinium distichum*, *Grindelia columbiana*, *Lomatium ambiguum*, *Microgilia micrantha*, *Navarretia leucocephala* subsp. *diffusa*, *Orthocarpus barbatus*, *O. tenuifolius*, *Polygonum polygaloides* subsp. *polygaloides*, and *Talinum spinescens*.

In Washington, many of the core native taxa are found almost exclusively in vernal pools. These include *Callitriche marginata*, *Camissonia tanacetifolia*, *Cuscuta cf. occidentalis*, *Elatine californica*, *E. chilensis*, *E. rubella*, *Juncus uncialis*, *Myosurus clavicaulis*, *Parietaria cf. hespera*, *Plagiobothrys* spp., *Polygonum polygaloides* subsp. *confertiflorum*, *P. polygaloides* subsp. *polygaloides*, *Psilocarphus brevissimus*, *P. elatior*, *P. oregonus*, *Trifolium cyathiferum*, and *Navarretia leucocephala* subsp. *diffusa*. The last of these was discovered and first described during this study (Björk 2002), and is endemic to the Columbia Plateau vernal pools. Other vernal pool taxa are disjunct from populations in vernal pools in the Columbia River Gorge or from farther south. These include *Alopecurus saccatus*, *Callitriche marginata*, *Downingia yina*, *Isoetes howellii*, *Juncus hemiendytus* var. *hemiendytus*, *J. uncialis*, *Myosurus clavicaulis*, *Navarretia leucocephala* subsp. *minima*, *Pilularia americana*, *Psilocarphus* spp., *Sclerolinon digynum*, and *Trichostema oblongum*.

Table 3. Per-pool taxon richness and total native richness reported from California pools and recorded in each subregion of the Columbia Plateau vernal pool province. Native and non-native richness values for east channel vernal pools are significantly different ($p < 0.01$) from those for west and central channel pools. *Barbour et al. 2003; Heise and Merenlender 1999; Holland 1976; Holland and Jain 1981. †Keeler-Wolf et al. 1998.

	Number of Species			
		Columbia Plateau, Washington		
	California	West Channel	Central Channel	East Channel
Per-pool richness				
Range	15–24*	20–51	22–86	12–59
Native (mean ± 1 SE)		35.9 ± 4.7	41.4 ± 1.9	22.2 ± 2.8
Non-native (mean ± 1 SE)		6.0 ± 1.0	4.7 ± 0.4	2.8 ± 0.5
Total native richness	367†	221	181	136

Vernal pools in the central flood channels had the largest flora, followed by pools in the eastern and lastly, the western subregions (Table 3). Some members of the core flora were found only in a single channel. Limited to the west subregion were *Callitriche hermaphroditica*, *Lotus denticulatus*, and *Orthocarpus barbatus*. The taxa *Cyperus squarrosus*, *Gayophytum ramosissimum*, *Lilaea scilloides*, *Lomatium bicolor* subsp. *leptocarpum*, *Navarretia leucocephala* subsp. *diffusa*, and *Psilocarphus tenellus* were found in vernal pools only in the central subregion. Limited to the east subregion were *Allium columbianum*, *Centaurium curvistamineum*, *Downingia elegans*, *Juncus hemiendytus* var. *hemiendytus*, *Ranunculus alismifolius* var. *alismifolius*, *Sclerolinon digynum*, and *Trichostema oblongum*.

Pools on the Columbia Plateau had a higher species richness than those in California (Table 3). Native taxon richness was highest in the central subregion and lowest in the east. The eastern subregion pools also had the fewest non-native taxa per pool (2.88 ± 0.47), significantly fewer than the western (6.00 ± 0.98; $p = 0.0053$) and central (4.75 ± 0.41) subregions. The presence of rare taxa did not differ significantly between the subregions.

DISCUSSION

The Columbia Plateau vernal pool region is noteworthy for its plant diversity and large number of pools. Also, the pools occur within a steppe

and woodland vegetation mosaic that, overall, is in good condition compared to the communities surrounding most of the California vernal pools. Despite their biotic richness and geographic extent, it is surprising that they have received so little scientific attention. The paucity of herbarium specimens in WS and WTU collected from the Columbia Plateau pools also indicates how little attention these pools have received.

The physical environment of the Columbia Plateau vernal pools resembles that of vernal pools in California. Both regions exhibit extreme seasonality in precipitation, producing similar hydrological cycles in the pools. Vernal pools in both regions have shallow and relatively inorganic soils, low to moderate alkalinity and salt concentration, and minimal thatch and soil-organic matter. Pools in the two regions share many species and genera, and those of the Columbia Plateau are dominated by annuals just as are the California vernal pools (Holland and Jain 1988; Zedler 1987). Collectively, these characters distinguish these west-coast vernal pools from other seasonally inundated, closed-basin wetlands that are termed vernal pools in other regions.

Comparisons between vernal pools on the Columbia Plateau and in California reveal some significant differences. Vernal pools in the California Floristic Province contain more species limited to vernal pool ecosystems and contain far more endemic taxa than those on the Columbia Plateau. This higher level of endemism probably reflects the greater antiquity of the California pools as compared to those in Washington, which originated no earlier than the later Missoula Flood events. However, per-pool species richness observed in California (Barbour et al. 2003; Heise and Merenlender 1999; Holland 1976; Holland and Jain 1981; Björk, unpubl. data) is lower than in Washington.

Several floristic elements appear to be unique to the Columbia Plateau pools. At least two dozen taxa that have not been documented in vernal pools elsewhere are common in the core flora, although many of these taxa do occur in other habitats. Particularly noteworthy is the tolerance of these species to the flood/desiccation cycles of Washington vernal pools and apparently not to similar hydrological patterns in California vernal pools. Likewise unique is the endemic plant known from the Columbia Plateau vernal pools, *Navarretia leucocephala* subsp. *diffusa*.

Vernal pools on the Columbia Plateau appear to be less threatened than in California. In the former, pools occur mostly in basalt-bedrock landscapes, where most development and agriculture would be impractical. Hence, it appears that there has been little outright eradication of pools. In contrast, development and agriculture have reduced vernal pools in California to an estimated 10% of original pre-European settlement

levels (Ferren and Fiedler 1993). Estimates of regional losses range from 66% in the Central Valley (Holland 1978) and 95–97% in San Diego County (Bauder et al. 1998) to total loss in Los Angeles, Orange, Riverside, and San Bernardino Counties (United States Fish and Wildlife Service 1993). Threats from non-native species also have been less pronounced on the Columbia Plateau. Although non-native taxa have had a major impact on the landscape surrounding many vernal pools on the Columbia Plateau, few sites are completely dominated by non-natives as has happened in the grasslands surrounding most of California's vernal pools (Zedler 1987). Our observations in Washington suggest that these vernal pools have been generally less invaded by non-native taxa than the surrounding communities, a pattern also reported in California (Holland and Jain 1981; Zedler 1987). Only a small percentage of Columbia Plateau pools have been heavily impacted by non-natives, which contrasts with pools in California, where most are heavily impacted by non-natives such as *Anagallis arvensis*, *Cotula coronopifolia*, *Erodium* spp., *Lolium* spp., *Lythrum hyssopifolium*, *Mentha pulegium*, *Polypogon* spp., and *Taeniatherum caput-medusae* (Barry 1998; Keeler-Wolf et al. 1998; Zedler 1987).

The extensive array of vernal pools in Washington represents a biologically significant resource that has been largely overlooked. Our investigations have uncovered numerous occurrences of plant species previously unrecorded in Washington. Given the lack of recognition of these habitats in the published literature, it is likely that there remain similar discoveries to be made among the very rich fauna that also occur in these systems. Future investigations of vernal pool biogeography, ecology, floristics, and fauna on the Columbia Plateau should encompass these important habitats.

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APPENDIX

SPECIES OF THE COLUMBIA PLATEAU VERNAL POOLS

Plant taxa of the Columbia Plateau vernal pools recorded in the 1997–1998 seasons. The symbols W, C, and E following the notes on each taxon indicate occurrence in the west, central, and east subregions, respectively. Non-core applies to taxa that are intolerant of the flood/desiccation cycle of vernal pools and which occurred as accidentals below the highest observed water levels. Non-native taxa are preceded by an asterisk (*). Collection numbers are those of the first author.

ISOETALES

ISOETACEAE. *Isoetes howellii* Engelm. – Occasional to locally common on basins; W, C, E.

FILICALES

DRYOPTERIDACEAE. *Woodsia oregana* D.C. Eaton – Rare on pool margins; flood-intolerant; non-core; W.

MARSILEACEAE. *Marsilea oligospora* Goodd. – Rare on basins; appears to be annual in vernal pools; C; *1259* (WS), *3233* (WTU). *Marsilea vestita* Hook. & Grev. – Occasional on basins; appears to be annual in vernal pools; C, E. *Pilularia americana* A. Br. – Rare on pool basins; C, E; *1261* (WS), *3287* (WTU).

ANTHOPHYTES

MONOCOTS

ALISMATACEAE. *Alisma gramineum* C.C. Gmel. – Rare in deep areas of large pools, where possibly annual; W, C, E. *Alisma triviale* Pursh – Rare in deep areas of large pools, where possibly annual; E. *Sagittaria cuneata* E. Sheldon – Rare in deep areas of large pools, where possibly annual; W.

ALLIACEAE. *Allium acuminatum* Hook. – Uncommon on margins; non-core; W, C, E. *Allium columbianum* (Ownbey & Mingrone) P.M. Peterson, Annable & Rieseberg – Locally common in shallow pools; on both margins and basins, less common in dry

uplands than in pools; E. *Allium geyeri* S. Watson var. *geyeri* – Very common on both margins and basins; W, C, E.

CYPERACEAE. *Bolboschoenus maritimus* (L.) Palla – Rare on basins of deep or expansive pools; W. *Carex athrostachya* Olney – Occasional on margins and basins; W, C, E. *Carex douglasii* Boott – Occasional on margins and basins where alkaline/salty; W, C, E. *Carex petasata* Dewey – Uncommon on pool margins, mostly where moderately alkaline; W. *Carex praegracilis* Boott – Uncommon on margins of alkaline pools; E. *Cyperus squarrosus* L. – Locally very common on basins, especially in the central subregion; C. *Eleocharis acicularis* (L.) Roem. & Schult. – Very common on basins, especially in deepest areas of pools; W, C, E. *Eleocharis bella* (Piper) Svenson – Rare on pool basins; C, E. *Eleocharis macrostachya* Britton – Very common in nearly all vernal pools, mostly on basins but sometimes spreading to margins; W, C, E. *Eleocharis parvula* (Roem. & Schult.) Link *ex* Bluff, Nees & Schauer – Rare on pool basins; W.

HYACINTHACEAE. *Camassia quamash* (Pursh) E. Greene var. *quamash* – Common on basins and margins; W, C, E.

IRIDACEAE. *Iris missouriensis* Nutt. – Occasional on margins, more common in more permanently moist areas like swales; C, E. *Sisyrinchium douglasii* A. Dietr. var. *inflatum* (Suksd.) P.K. Holmgr. – Occasional on margins; E. *Sisyrinchium halophilum* E. Greene – Occasional on margins of alkaline/salty pools, more common on salt flat margins; non-core; C; *6207* (WS). *Sisyrinchium idahoense* E.P. Bicknell – Occasional on margins; non-core; C.

JUNCACEAE. *Juncus acuminatus* Michx. – Occasional on margins; E. *Juncus arcticus* Willd. var. *mexicanus* (Willd. *ex* Schult. & Schult. f.) Balslev – Common on margins; W, C, E. *Juncus bufonius* L. var. *bufonius* – Very common on basins; W, C, E. *Juncus bufonius* L. var. *occidentalis* F.J. Herm. – Less common than var. *bufonius* and usually growing with it; W, C, E; *3033* (WS), *3227, 3286* (WTU). *Juncus dudleyi* Wieg. – Occasional on margins; C, E. *Juncus hemiendytus* F.J. Herm. var. *hemiendytus* – Rare on basins; E; *3037, 3205, 3214* (WTU). *Juncus nevadensis* S. Watson – Uncommon on margins; W, C. *Juncus uncialis* E. Greene – Rare on basins; W, C, E; *3038* (WS), *3036, 3209, 3289, 3314* (WTU).

JUNCAGINACEAE. *Lilaea scilloides* (Poir.) Hauman – Rare on basins in mostly large pools; C; *1895* (WS).

POACEAE. *Achnatherum thurberianum* (Piper) Barkworth – Rare on margins; non-core; C. *Agrostis diegoensis* Vasey – Common on margins, uncommon on basins; W, C, E. *Agrostis exarata* Trin. – Uncommon on margins; C. **Agrostis stolonifera* L. – Uncommon on margins, usually where alkaline/salty; C. *Alopecurus carolinianus* Walter – Common on basins; C, E; *3158* (WTU). *Alopecurus saccatus* Vasey – Common on basins; intergrading with *A. carolinianus*; W, C, E; *3327* (WTU), *3886, 6198* (WS). **Apera interrupta* (L.) P. Beauv. – Very common on margins; one of the most abundant plants seen in the region in the cool, wet 1997 season, but dramatically less common in the dry, hot 1998 season; W, C, E. *Beckmannia sizygachne* (Steud.) Fernald – Occasional on basins; E. **Bromus hordaceus* L. – Very common on

margins; W, C, E. **Bromus tectorum* L. – Uncommon on margins; apparently flood-intolerant; W, C, E. *Calamagrostis rubescens* Buckley – Locally common around margins; E. *Critesion californicum* (Covas & Stebbins) Á. Löve – Common on margins and basins; W, C, E; *6210* (WS). *Critesion depressum* (Scribn. & J.G. Sm.) Á. Löve – Uncommon on margins and basins; W, C. *Critesion jubatum* (L.) Nevski – Common on margins and basins; W, C, E. *Danthonia californica* Bol. subsp. *californica* – Occasional on margins; E. *Danthonia unispicata* (Thurb.) Munro *ex* Macoun – Common on margins, occasional on basins; W, C, E. *Deschampsia cespitosa* (L.) P. Beauv. – Uncommon on margins; E. *Deschampsia danthonioides* (Trin.) Munro *ex* Benth. – Very common on basins, but mostly not in pool center; W, C, E. *Distichlis spicata* (L.) E. Greene – Common on basins and margins of alkaline/salty pools; W, C; *6211* (WS). *Elymus elymoides* (Raf.) Swezey – Occasional on margins, uncommon on basins; C, E. **Elytrigia repens* (L.) Desv. *ex* B.D. Jacks. – Common in disturbed pools, growing on basins and margins; W, C, E. *Festuca idahoensis* Elmer – Common near margins, but not flood-tolerant; non-core; C. *Festuca rubra* L. Common near margins, flood-intolerant; non-core; C. *Leymus cinereus* (Scribn. & Merr.) Á. Löve Very common on margins; W, C, E. *Leymus* sp. – One population on the floor of a very large pool; C; *3252* (WTU). *Muhlenbergia asperifolia* (Nees & Meyen *ex* Trin.) Parodi – Occasional in alkaline/salty pools; C. *Muhlenbergia richardsonis* (Trin.) Rydb. – Common on basins and margins; W, C, E. *Panicum capillare* L. – Common on basins and margins, germinating post-desiccation; C, E. *Pascopyrum smithii* (Rydb.) Barkworth & D.R. Dewey – Uncommon on basins and margins, mostly in alkaline/salty pools; C. **Phalaris arundinacea* L. – Occasional on margins and basins of disturbed pools; E. **Phleum pratense* L. – Uncommon on margins and basins, probably growing only where sowed for forage; E. **Poa bulbosa* L. – Common on margins; W, C, E. **Poa compressa* L. – Common on basins of east subregion pools, in both disturbed and pristine pools; W, C, E. *Poa juncifolia* Scribn. – Rare on margins of alkaline/salty pools; non-core; C. **Poa pratensis* L. – Uncommon on margins and basins, mostly where disturbed; W, E. *Poa scabrella* (Thurb.) Benth. *ex* Vasey – Very common on margins, uncommon on basins; W, C, E. **Polypogon monspeliensis* (L.) Desf. – Common on margins and basins of alkaline/salty pools; W, C. *Pseudoroegneria spicata* (Pursh) Á. Löve – Flood intolerant, occasional along pool margins; non-core; W, C, E. **Puccinellia distans* (Jacq.) Parl. – Occasional on margins and basins of alkaline/salty pools; W; *3200* (WTU). *Puccinellia nuttalliana* (Schult.) Hitchc. – Occasional on margins and basins of alkaline/salty pools; C. *Sphenopholis obtusata* (Michx.) Scribn. – Rare on basins, limited to alkaline/salty pools; C. **Taeniatherum caput-medusae* (L.) Nevski – Locally common on margins; W, C, E. **Triticum* cultivar (seedlings) – Uncommon on basins, mostly in roadside pools; germinating post-desiccation and never reaching maturity; intolerant of summer drought; non-core; C, E. *Vulpia octoflora* (Walter) Rydb. – Rare on margins; non-core; C.

POTAMOGETONACEAE. *Stuckenia pectinata* (L.) Börner – Rare on basins of deep, alkaline/salty pools; W.

TYPHACEAE. *Typha latifolia* L. (seedlings only) – Occasional on basins; always dying from drought in the first season before reaching maturity; non-core; C, E.

ZANNICHELLIACEAE. *Zannichellia palustris* L. – Rare in deep pools; W.

EUDICOTS

AMARANTHACEAE. **Amaranthus albus* L. – Occasional summer annual on pool basins, germinating post-desiccation; W, C, E. *Amaranthus californicus* (Moq.) S. Watson – Locally common on pool basins; E. *Amaranthus graecicans* S. Watson – Common summer annual of pool basins, germinating post-desiccation; W, C, E. *Atriplex truncata* (Torr. *ex* S. Watson) A. Gray – Occasional in alkaline/salty pools; W, C. *Chenopodium rubrum* L. – Rare on basins in alkaline/salty pools; C. *Chenopodium* sp. (*C. album* complex) – Occasional on margins; non-core; E. *Monolepis nuttalliana* (Schult.) E. Greene – A single plant found on a post-desiccation pool floor; C. *Suaeda calceoliformis* (Hook.) Moq. – Rare on margins of alkaline/salty pools; C.

APIACEAE. *Lomatium ambiguum* (Nutt.) J.M. Coult. & Rose – Occasional on margins; common on Mima mounds surrounding vernal pools; non-core; W, C, E. *Lomatium bicolor* (S. Watson) J.M. Coult. & Rose subsp. *leptocarpum* (Nutt. *ex* Torr. & A. Gray) Schlessman – Locally common on margins and basins; C; *3391* (WS). *Lomatium grayi* (J.M. Coult. & Rose) J.M. Coult. & Rose – Locally common on margins and basins; equally common in pools and in surrounding grasslands; W, C, E. *Lomatium macrocarpum* (Nutt. *in* Torr. & A. Gray) J.M. Coult. & Rose – Occasional on margins; flood-intolerant; non-core; W, C, E. *Perideridia montana* (Blank.) Dorn – Common on margins in all three subregions, very common on Mima mounds surrounding vernal pools; W, C, E.

APOCYNACEAE. *Asclepias speciosa* Torr. – Rare on margins; non-core; W, C, E.

ASTERACEAE. *Achillea millefolium* L. – Common on margins, occasional on basins; the local form is flood-tolerant; W, C, E. *Agoseris grandiflora* (Nutt.) E. Greene – Occasional on margins, locally common on Mima mounds surrounding vernal pools; non-core; C. *Agoseris heterophylla* (Nutt.) E. Greene – Occasional, mostly on margins; W, C, E. *Ambrosia* sp. – A single occurrence on margins of an alkaline pool; non-core; E. *Antennaria luzuloides* Torr. & A. Gray – Rarely found on pool margins, very common on surrounding lithosol; flood-intolerant; non-core; E. *Antennaria stenophylla* (A. Gray) A. Gray – Rare on pool margins; flood-intolerant; non-core; C. *Arnica fulgens* Pursh – Rare on margins, occasional in surrounding grassland; non-core; C (W, E?). *Arnica sororia* E. Greene – Rare on margins, occasional in surrounding grassland; non-core; W, E (C?). *Artemisia biennis* Willd. – Occasionally found in alkaline pools; W, C. *Artemisia ludoviciana* Nutt. var. *ludoviciana* – Common on margins and basins; flood-tolerant; W, C, E. *Artemisia rigida* (Nutt.) A. Gray – Rare on margins, common on lithosol surrounding rocky pools, flood-intolerant; non-core; C. *Artemisia tridentata* Nutt. subsp. *tridentata* – Common around pools; flood intolerant, germinates occasionally in pools post-desiccation and with the first fall rains, but is later killed in high water; W, C, E. *Artemisia tripartita* Rydb. – Rare on margins, flood-intolerant; non-core; C. **Centaurea* spp. – Rare on margins, mostly where disturbed; common in local outbreaks in surrounding grassland, mostly where grazing is heavy; non-core; W. *Chamomilla suaveolens* (Pursh) Rydb. – Occasional on pool basins and margins; often very robust and semi-succulent when growing in alkaline/salty pools; C, E. *Chrysothamnus nauseosus* (Pall. *ex* Pursh) Britton – Rare on margins; flood-intolerant; C. **Cirsium arvense* (L.) Scop. – Occasional on margins and

basins, mostly where disturbed; moderately flood-tolerant; W, C, E. *Cirsium brevifolium* Nutt. – Occasional on pool margins, more common beyond pool margins on tops of Mima mounds; apparently tolerant of brief flooding; C, E. **Cirsium vulgare* (Savi) Ten. – Uncommon on pool margins, mostly where disturbed; non-core; W, C, E. *Conyza canadensis* (L.) Cronq. – Common on margins and basins, germinating post-desiccation; W, C. E. *Erigeron corymbosus* Nutt. – Rare on margins; non-core; C. *Erigeron pumilus* Nutt. subsp. *intermedius* Cronq. var. *gracilior* Cronq. – Rare on margins; flood-intolerant; non-core; C, E. **Filago arvensis* L. – Uncommon on margins; C, E. *Gaillardia aristata* Pursh – Occasional on margins, common on Mima mounds surrounding vernal pools; flood intolerant; non-core; W, C, E. *Gnaphalium palustre* Nutt. – Very common on basins, occasional on margins; W, C, E. *Grindelia columbiana* (Piper) Rydb. – Common in central and west subregions, on basins and margins, equally common in pools and in surrounding grasslands; possibly just a rayless form of *G. nana*; W, C. *Grindelia nana* Nutt. – Common on basins and margins, equally common in pools and in surrounding grasslands; C, E. *Helianthus annuus* L. – Occasional, germinating on basins post-desiccation; usually dies from drought before flowering; W, E. *Iva axillaris* Pursh – Occasional on margins of alkaline/salty pools, much more common in and around more permanent wetlands; W, C. **Lactuca serriola* L. – Common on margins and basins, mostly germinating post-desiccation; highly drought-tolerant, flowering well into autumn; W, C, E. *Lactuca tatarica* (L.) C.A. Mey. subsp. *pulchella* (Pursh) Stebb. – Rare on margins, more common on Mima mounds surrounding vernal pools; non-core; C, E. *Lagophylla ramosissima* Nutt. – Common on margins, more so than in surrounding grasslands; C. *Madia exigua* (Sm.) A. Gray – Very common on margins; typically growing at higher densities on pool margins than in surrounding grasslands; W, C, E. *Madia glomerata* Hook. – Common on margins; typically growing at higher densities on pool margins than in surrounding grasslands; W, C, E. *Madia gracilis* (Sm.) D.D. Keck – Common on margins; typically growing at higher densities on pool margins than in surrounding grasslands; C, E. *Microseris nutans* (Hook.) Sch.Bip. – Occasional on margins; flood-intolerant; non-core; C. *Nothocalais troximoides* (A. Gray) E. Greene – Rare on margins; non-core; C. *Psilocarphus brevissimus* Nutt. – Very common on pool basins; often intergrading with *P. elatior*; W, C, E. *Psilocarphus elatior* A. Gray – Very common on pool basins; often intergrading with *P. brevissimus*; C, E. *Psilocarphus oregonus* Nutt. – Very common on pool basins; W, C, E; *3216* (WTU). *Psilocarphus tenellus* Nutt. – Rare; found in only two pools, both having unusual cherty-clay soil; C, E; *3390* (WTU). *Senecio hydrophiloides* Rydb. – Common on margins, locally very common in seasonally wet meadows surrounding vernal pools; C, E. *Senecio integerrimus* Nutt. – Occasional on margins, common on Mima mounds surrounding vernal pools; non-core; C, W. *Senecio serra* Hook. – Occasional on margins, very common on Mima mounds surrounding vernal pools; non-core; C. **Sonchus asper* (L.) Hill – Occasional on margins and basins, germinating post-desiccation; C. **Taraxacum officinalis* Weber *ex* F.H. Wigg. – Rare on margins; flood-intolerant; common in surrounding grasslands where heavily grazed; non-core; W, C, E. **Tragopogon dubius* Scop. – Occasional on margins; non-core; C, W. *Xanthium strumarium* L. – Rare on basins, germinating post-desiccation; W.

BORAGINACEAE. *Amsinckia lycopsoides* Lehm. – Common on margins, growing at higher densities on pool margins than in surrounding grasslands; W, C, E. *Amsinckia menziesii* (Lehm.) A. Nels. & J.F. Macbr. var. *intermedia* (Fischer & C.A. Mey.)

Ganders – Occasional on margins, more common on Mima mounds surrounding vernal pools; C, E. *Amsinckia menziesii* (Lehm.) A. Nels. & J.F. Macbr. var. *menziesii* – Occasional on margins, more common on Mima mounds surrounding vernal pools; C, E. *Amsinckia retrorsa* Suksd. – Common on margins, growing at higher densities on pool margins than in surrounding grasslands; W, C, E. **Anchusa officinalis* L. – Rare on margins; non-core; E. *Cryptantha torreyana* (A. Gray) E. Greene – Occasional on margins; W, C, E. *Hesperochiron californicus* (Benth.) S. Watson – Occasional on margins, mostly around alkaline/salty pools; W, C, E. *Lappula redowskii* (Hornem.) E. Greene – Occasional on margins; flood-intolerant; non-core; C. **Lithospermum arvense* L. – Rare on margins; flood-intolerant; non-core; E. **Myosotis micrantha* Pall. *ex* Lehm. – Occasional on margins; C, E. *Myosotis verna* Nutt. – Occasional on margins, more common on Mima mounds and lithosols surrounding vernal pools; C, E. *Plagiobothrys leptocladus* (E. Greene) I.M. Johnston – Very common on basins, commonest in west and central subregions; W, C, E. *Plagiobothrys* spp. [*P. bracteatus* (T.J. Howell) I.M. Johnston; *P. cognatus* (E. Greene) I.M. Johnston; *P. cusickii* (E. Greene) I.M. Johnston, *1675*, *1676* (WS); *P. hispidulus* (E. Greene) I.M. Johnston; *P. scouleri* (Hook. & Arn.) I.M. Johnston; *P. stipitatus* (E. Greene) I.M. Johnston, *1670* (WS); *P. tener* (E. Greene) I.M. Johnston, *1669* (WS)] – Locally very common; more work is needed to sort out the diversity of this complex in the Columbia Plateau pools, fragrance as well as corolla size and coloration in at least some populations vary between wet/cool and hot/dry climatic periods; W, C, E.

BRASSICACEAE. *Arabis nuttallii* B.L. Rob. – Rare on margins, more common in swales and wet meadows; C. *Arabis sparsiflora* Nutt. – Rare on margins; flood-intolerant; non-core; C. *Barbarea orthoceras* Ledeb. – Locally common on margins and basins; E. **Capsella bursa-pastoris* (L.) Medik. – Rare on margins; non-core; C. *Cardamine oligosperma* Nutt. – Rare on margins and basins; E. **Descurainia sophia* (L.) Webb *in* Engl. & Prantl – Occasional on margins, mostly where disturbed; non-core; C. *Draba verna* L. – Occasional on margins; flood-intolerant; very common beyond high water mark on both lithosols and deeper soils surrounding vernal pools; W, C, E. *Erysimum cheiranthoides* L. – Rare on pool basins; E. *Idahoa scapigera* (Hook.) A. Nels. & J.F. Macbr. – Occasional on margins, much more common on winter-wet lithosols surrounding vernal pools; C, E. **Lepidium perfoliatum* L. – Occasional on margins, most common where alkaline/salty; W, C, E. *Lepidium* spp. – Rare on margins; non-core; W. *Rorippa curvisiliqua* (Hook.) Bessey *ex* Britton – Very common on basins; germinating both pre- and post-desiccation and acting either as an annual or a biennial; W, C, E. **Sisymbrium altissimum* L. – Common on margins, particularly where disturbed; flood-intolerant; G; germinating post-desiccation; very common in surrounding grasslands, especially where disturbed; non-core; W, C, E.

CAMPANULACEAE. *Downingia elegans* (Dougl. *ex* Lindl.) Torr. – Common on basins; E. *Downingia yina* Applegate – Common on basins, mostly in west and central subregions; highly variable throughout the full range, but uniform across the Columbia Plateau; W, C, E; *3282*, *3443* (WTU). *Heterocodon rariflorum* Nutt. – Occasional on margins and basins; C, E.

CAPRIFOLIACEAE. *Symphoricarpos albus* (L.) S.F. Blake – Rare on margins, flood-intolerant; non-core; C, E.

CARYOPHYLLACEAE. *Cerastium nutans* Raf. – Occasional on margins; W, C, E. **Holosteum umbellatum* L. – Occasional on margins; very common in surrounding grasslands; W, C, E. **Spergularia bocconii* (Scheele) Foucaud – Occasional on basins; W, C, E. *Spergularia maritima* (All.) Chiov. – Very common on basins; C, E. **Spergularia rubra* (L.) J. Presl & C. Presl – Rare on basins and margins; W.

CLUSIACEAE. **Hypericum perforatum* L. – Rare on margins; locally very common in surrounding grasslands, particularly on Mima mounds surrounding vernal pools; non-core; E.

CONVOLVULACEAE. **Convolvulus arvensis* L. – Locally common on basins and margins; E. *Cuscuta occidentalis* Millsp. – Uncommon, most often on margins, but apparently never in upland areas beyond the pools; parasitizes a wide variety of hosts; W, C; *3156*, *3369* (WTU).

ELATINACEAE. *Elatine californica* A. Gray – Occasional on pool basins; W, C, E. *Elatine chilensis* Gay and/or *E. rubella* Rydb. – Rare on pool basins; C, E; *1383* (WS).

EUPHORBIACEAE. *Chamaesyce serpyllifolia* (Pers.) Sm. – Common on pool basins, germinating post-desiccation; W, C, E.

FABACEAE. *Astragalus agrestis* Dougl. *ex* Hook. – Occasional on margins, mostly where alkaline/salty; C. *Lotus denticulatus* (Drew) E. Greene – Locally common on margins; W; *1498* (WS). *Lotus purshiana* (Benth) F. Clements & E. Clements – Very common on margins; W, C, E. *Lupinus* spp. – Uncommon on margins; all local species apparently flood-intolerant; very common in surrounding grasslands; non-core; W, C. **Medicago lupulina* L. – Occasional on margins, and germinating on basins post-desiccation; flood-intolerant; non-core; W, C, E. **Melilotus* spp. – Uncommon on margins and germinating on basins post-desiccation; flood-intolerant; apparently always dying of drought in vernal pools before the end of summer; non-core; W, C, E. *Trifolium cyathiferum* Lindl. – Common on margins; W, C, E. **Trifolium dubium* Sibth. – Uncommon on margins; apparently flood-intolerant; non-core; W, C, E. *Trifolium microcephalum* Pursh – Common on margins; W, C, E. *Trifolium variegatum* Nutt. *ex* Torr. & A. Gray – Common on margins; W, C, E. **Vicia villosa* Roth – Rare on margins; C, E.

GENTIANACEAE. *Centaurium curvistamineum* (Wittr.) Abrams – Locally common on basins and margins; E; *3441* (WTU). *Centaurium exaltatum* (Griseb.) W. Wight *ex* Piper – Occasional on basins and margins of alkaline/salty pools; W, C.

GERANIACEAE. *Geranium bicknellii* Britton – Common on basins and margins; germinating post-desiccation; W, C, E.

GROSSULARIACEAE. *Ribes cereum* Dougl. var. *cereum* – Rare on margins, flood-intolerant; non-core; C.

LAMIACEAE. *Mentha arvensis* L. – Rare on margins mostly of very large pools; flood-tolerant, but apparently not highly tolerant of the drought stage in vernal pools;

C. *Trichostema oblongum* Benth. – Rare in small, cobbly pools; E; *3221* (WTU), *6212* (WS).

LINACEAE. *Linum lewisii* Pursh – Uncommon on margins; non-core; C. *Sclerolinon digynum* (A. Gray) C.M. Rogers – Rare on margins; E; *3222, 3447* (WTU), *6208* (WS).

LOASACEAE. *Mentzelia dispersa* S. Watson – Rare on margins; non-core; E.

LYTHRACEAE. *Ammannia robusta* Heer & Regel – Rare on pool basins in the east subregion; non-core; found only in two pools adjacent to permanent lakes; E; *3451* (WTU).

MALVACEAE. *Sidalcea oregana* (Nutt. *ex* Torr. & A. Gray) A. Gray var. *maxima* (M.E. Peck) C.L. Hitchc. – Occasional on margins; plants of some populations around western pools are very robust, producing stout horizontal rhizomes and growing as tall as 1.5 m; W, C. *Sidalcea oregana* (Nutt. *ex* Torr. & A. Gray) A. Gray var. *procera* C.L. Hitchc. – Occasional on margins; W, C, E.

MYRSINACEAE. *Anagallis minima* (L.) E.H.L. Krause – Occasional on basins and margins, particularly where alkaline/salty; W, C, E; *3223* (WTU).

ONAGRACEAE. *Boisduvalia densiflora* (Lindl.) S. Watson – Very common on basins and margins; W, C, E. *Boisduvalia glabella* (Nutt.) Walp. – Very common on basins, especially in deep areas; W, C, E. *Boisduvalia stricta* (A. Gray) E. Greene – Uncommon on basins and margins; W, C, E. *Camissonia andina* (Nutt.) P.H. Raven – Occasional on basins and margins; C, E. *Camissonia hilgardii* (E. Greene) P.H. Raven – Rare on basins and margins; may be just a large-flowered form of *C. andina*; W, C; *1554* (WS), *3286* (WTU). *Camissonia tanacetifolia* (Torr. & A. Gray) P.H. Raven – Occasional on basins; C, E; *1555* (WS). *Clarkia pulchella* Pursh – Common on margins; very abundant in 1997 but far less so in 1998; W, C, E. *Epilobium brachycarpum* C. Presl – Very common on margins; W, C, E. *Epilobium* spp. – Occasional on margins; W, C. *Gayophytum ramosissimum* Torr. & A. Gray – Rare on basins of pools having cherty-clay soil; C.

OROBANCHACEAE. *Castilleja minor* (A. Gray) A. Gray subsp. *minor* – Occasional on margins where alkaline/salty; W, C; *3446* (WTU). *Castilleja tenuis* (A.A. Heller) Chuang & Heckard – Very common on margins, uncommon on basins; W, C, E; *6192* (WS). *Orthocarpus barbatus* J.S. Cotton – Uncommon on margins; W. *Orthocarpus tenuifolius* (Pursh) Benth. - Common on margins; W, C, E.

PHRYMATACEAE. *Mimulus breviflorus* Piper – Occasional on margins and basins; W, C, E. *Mimulus floribundus* Dougl. *ex* Lindl. – Occasional on margins, grows extremely robustly around alkaline/salty pools; W, C; *3334* (WTU). *Mimulus guttatus* Fisch. *ex* DC. – Occasional on margins; unlike in California, the Scabland form of this species does not appear to tolerate the pool-floor habitat; W, C, E. *Mimulus suksdorfii* A. Gray – Rare on margins; W; *3283* (WTU).

PLANTAGINACEAE. *Callitriche hermaphroditica* L. – Found only in one moderately alkaline pool in the Grand Coulee; W. *Callitriche marginata* Torr. – Uncommon on

basins, mostly in deep or expansive pools; C, E; *1693* (WS), *3288* (WTU). *Collinsia parviflora* Dougl. *ex* Lindl. – Occasional on margins; E. *Gratiola ebracteata* Benth. – Common on basins; C, E. *Gratiola neglecta* Torr. – Rare on basins; E. *Limosella aquatica* L. – Very common on basins; W, C, E. *Penstemon procerus* Dougl. *ex* Graham – Rare on margins; non-core; C, E. **Plantago major* L. – Uncommon on margins and basins; native in part; C. *Plantago patagonica* Jacq. – Very common, mostly on margins; W, C, E. **Veronica arvensis* L. – Rare on margins; non-core; E. *Veronica peregrina* L. var. *xalapensis* Kunth – Very common, mostly on basins; W, C, E.

POLEMONIACEAE. *Collomia linearis* Nutt. – Uncommon on margins; non-core; C, E. *Microgilia minutiflora* (Benth.) J.M. Porter & L.A. Johnson – Rare on basins of pools having a cherty-clay soil; C. *Microsteris gracilis* (Hook.) E. Greene – Very common on margins, especially in the east subregion; sometimes forming dense populations of tall, robust plants having relatively large, fragrant flowers; W, C, E. *Navarretia intertexta* (Benth.) Hook. – Common on margins; subspp. *intertexta* and *propinqua* intergrade locally, and some populations cannot be assigned to one or the other subspecies; W, C, E; *3231* (WTU). *Navarretia leucocephala* Benth. subsp. *diffusa* Björk – Very common on basins only in central Lincoln County (the northern central-subregion pools), where growing to the exclusion of subsp. *minima*; C; *3228, 3250* (WTU). *Navarretia leucocephala* Benth. subsp. *minima* (Nutt.) A.G. Day – Very common on basins, not occurring in the range of subsp. *diffusa*; W, C (southern portions), E; *3204* (WTU). *Phlox longifolia* Nutt. – Rare on margins; flood-intolerant; non-core; W, C.

POLYGONACEAE. *Eriogonum compositum* Dougl. *ex* Benth. – Occasional on margins of central and east subregion pools, where the local form is flood-tolerant; C, E. *Eriogonum heracleoides* Nutt. – Occasional on margins, especially in the west subregion pools; the local form is flood-tolerant; W, C, E. *Eriogonum niveum* Dougl. *ex* Benth. – Rare on margins, apparently flood-intolerant; non-core; C. *Eriogonum thymoides* Benth. – Uncommon on margins of the central and west subregion pools; apparently flood-intolerant; non-core; C. *Polygonum achoreum* S.F. Blake – Very common on basins and margins; germinating post-desiccation; W, C, E. *Polygonum douglasii* E. Greene subspp. – Uncommon on margins; flood intolerant; non-core; W, C, E. *Polygonum polygaloides* Meisn. subsp. *confertiflorum* (Nutt. *ex* Piper) J.C. Hickman – Very common on basins and margins, especially in the central and west subregions [some populations in eastern pools may be attributable to subsp. *esotericum* (L.C. Wheeler) J.C. Hickman, a rare regional endemic of northern California; wider sampling is needed to determine the identity of these populations]; W, C, E; *1362* (WS). *Polygonum polygaloides* Meisn. subsp. *polygaloides* – Very common on basins and margins, especially in the east subregion, where growing in very dense, showy light-pink displays and sometimes producing a sweet fragrance, attracting abundant pollinators; C, E. **Rumex crispus* L. – Occasional on basins and margins; W, C, E. *Rumex maritimus* L. – Uncommon on basins of alkaline/salty pools; W, C, E. **Rumex patientia* L. – Rare on margins and basins; C. *Rumex salicifolius* Weinm. – Common, mostly on basins; W, C, E.

PORTULACACEAE. *Montia dichotoma* (Nutt.) Howell – Very common on margins; some populations in the central region grow across pool basins; C, E. *Montia linearis*

(Dougl. *ex* Hook.) E. Greene – Occasional on rocky margins; C, E. *Talinum spinescens* Torr. – Occasional on margins; some populations are flood-tolerant and grow across pool basins; W, C.

PRIMULACEAE. *Dodecatheon* sp. – Rare on margins; flood-intolerant; non-core; W.

RANUNCULACEAE. *Delphinium distichum* Geyer *ex* Hook. – Occasional or locally common on margins; W, C, E. *Myosurus apetalus* Gay var. *borealis* Whittem. – Occasional on margins; C. *Myosurus clavicaulis* M. Peck – Rare on basins; no intermediates with *M. minimus* found, though in California, this species is known to hybridize with its putative parent species, *M. minimus* and *M. sessilis* S. Watson; this appears to be a stable species in eastern Washington; W, C, E; *3210, 3215, 3315* (WTU). *Myosurus minimus* L. subsp. *minimus* – Very common on basins; W, C, E. *Ranunculus alismifolius* Geyer *ex* Benth. var. *alismifolius* – Found in a single pool, where dominant; E. *Ranunculus aquatilis* L. – Rare on basins of deep pools; W, C, E; *1277* (WS). *Ranunculus sceleratus* L. – Rare on basins of deep pools; C. **Ranunculus testiculatus* Crantz – Rare on margins; C.

ROSACEAE. *Amelanchier alnifolia* (Nutt.) Nutt. – Rare on margins; flood intolerant; non-core; W. *Geum triflorum* Pursh var. *triflorum* – Rare on margins, common in surrounding grasslands; flood intolerant; non-core; C. *Potentilla gracilis* Dougl. *ex* Hook. – Rare on margins, common in surrounding grasslands; flood-intolerant; non-core; W, C, E. *Potentilla rivalis* Nutt. – Occasional on basins of deep pools; C. *Rosa woodsii* Lindl. – Rare on margins, common in surrounding grasslands; probably flood-intolerant; non-core; C, E. *Sanguisorba occidentalis* Nutt. – Common on basins, occasional on margins; mostly germinating post-desiccation and over-wintering as flooded rosettes to bloom the following summer; C, E.

RUBIACEAE. *Galium aparine* L. – Uncommon on margins, but very common on Mima mounds surrounding pools; flood-intolerant; non-core; W, C, E. *Galium trifidum* L. – Rare on basins; E.

SARCOBATACEAE. *Sarcobatus vermiculatus* (Hook.) Torr. – Rare on margins of alkaline/salty vernal pools; non-core; C, W.

SAXIFRAGACEAE. *Lithophragma glabrum* Nutt. – Rare on margins, but common on Mima mounds surrounding pools; flood-intolerant; non-core; C.

URTICACEAE. *Parietaria* cf. *hespera* B.D. Hinton – Uncommon on margins, but not highly flood-tolerant; occasional in surrounding grasslands; W, C, E; *3313* (WTU), *6216* (WS).

VALERIANACEAE. *Plectritis macrocera* Torr. & A. Gray – Occasional on margins; C.

VERBENACEAE. *Verbena bracteata* Lag. & Rodr. – Rare on margins or basins, germinating post-desiccation; flood-intolerant; non-core; C, W.

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TAXONOMIC REVISION OF THE GENUS *PSEUDOSMODINGIUM* (ANACARDIACEAE)

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ABSTRACT. A taxonomic treatment of the genus *Pseudosmodingium* (Anacardiaceae) is presented. The genus consists of four extant and two fossil species endemic to Mexico. The extant species are small trees from tropical dry forests. The two fossil species have been described from Oligocene strata from Puebla in Central Mexico. Among extant species, *P. andrieuxii* and *P. multifolium* were considered previously as separate taxa; however, we concluded based on both vegetative and floral characters that they can be assigned to the same species, *P. andrieuxii*. The rest of the species (*P. barkleyi*, *P. perniciosum*, and *P. virletii*) are very similar to one another in floral morphology, but variable in leaf morphology. Comments, descriptions, additional notes, specimen citations, distribution, diagnoses, and a key for the extant species of *Pseudosmodingium* are presented.

Key Words: *Pseudosmodingium*, Anacardiaceae, Mexico

Pseudosmodingium Engl. is a small genus of four extant and two fossil species endemic to Mexico. The extant species are small trees from tropical dry forests, characterized by having imparipinnate leaves, paniculate inflorescences with unisexual and bisexual flowers, and a drupe with two chartaceous wings. All extant species of *Pseudosmodingium* contain toxic catechols (urushiols) in the leaves and bark, causing contact dermatitis (Aguilar-Ortigoza et al. 2003). The two fossil species (*P. mirandae* Ramírez et al. and *P. terrazasiae* Ramírez et al.) have been collected in Oligocene strata of Puebla in Central Mexico (Ramírez-Garduño et al. 2000). The abundance of fossils of *Pseudosmodingium* in these strata suggests a Tertiary origin of the genus (Ramírez-Garduño et al. 2000). The place of origin of the genus was most likely in the dry zones of central Mexico according to results of phylogenetic studies, since *Pseudosmodingium* is grouped with taxa from these areas (Aguilar-Ortigoza and Sosa 2004).

Initially, Baillon (1874) included within the South African genus *Smodingium* E. Mey., the two species *S. andrieuxii* Baill. and *S. virletii* Baill. because their drupes are winged, as in *S. argutum* E. Mey. Later, Engler (1881) segregated these two species into the genus *Pseudosmodingium* based on characters such as a 3-branched style and an anatropous ovule inserted at the base of the ovary. *Rhus perniciosa*, described by Humboldt, Bonpland, and Kunth in 1825, was also transferred to *Pseudosmodingium* based on the morphology of the fruit (Barkley and Reed 1940). Several other species were subsequently described in *Pseudosmodingium*: *P. multifolium* Rose (Rose 1897), *P. rhoifolium* (DC.) F.A. Barkley (Barkley 1937), and *P. barkleyi* Miranda (Miranda 1961). Johnston (1946) described *P. anomalum* I.M. Johnst. without certainty of its position because of the lack of drupes in the type collection. This species was later segregated by Rzedowski (1957) into *Bonetiella* Rzed. because it possessed simple leaves and a wingless fruit.

The remaining species of *Pseudosmodingium* constitute a monophyletic group (Aguilar-Ortigoza et al. 2004). Among synapomorphic characters to define the genus are leaflets showing incomplete marginal venation and leaves grouped at the apex of branches, flowers with valvate sepals, oblong petals, filiform stamens, spheroidal pollen, flower disc with a lobate margin, fruit oblate, seeds with a crustaceous testa, and wood lacking growth rings (Aguilar-Ortigoza et al. 2004). Two groups of species are recognized in the genus, one formed by the fossil species *P. terrazasieae* and *P. mirandae*, together with the living *P. andrieuxii*. Advanced characters shared in this grouping are leaf characters such as outline, margin, venation, and pubescence. These characters were observed in the fossil species from cellulose acetate films prepared from paleobotanical vouchers (Aguilar-Ortigoza et al. 2004). The other group in the genus is formed by *P. perniciosum*, *P. barkleyi*, and *P. virletii*, in which synapomorphic characters are coriaceous leaves with a hypodermis, but without capitate trichomes on the abaxial surface of the leaves, and a wood with procumbent cells in the rays (Aguilar-Ortigoza et al. 2004).

Engler (1881) divided Anacardiaceae into five tribes and classified *Pseudosmodingium* in tribe Rhoeae. In this tribe, several genera in addition to *Pseudosmodingium* possess winged fruits, among them are *Smodingium*, *Cardenasiodendron* F.A. Barkley, and *Loxopterygium* Hook. f. (Barkley 1954, 1962). However, *Pseudosmodingium* is not likely related to the other three genera. A phylogenetic analysis using morphological and anatomical characters showed *Smodingium* and

Cardenasiodendron to be closely related to one another, but not to *Pseudosmodingium* (Aguilar-Ortigoza et al. 2004; *Loxopterygium* was not included in this study). Another study, in which species diversification was analyzed using nuclear ribosomal ITS sequences, showed *Cardenasiodendron* and *Loxopterygium* to be sister taxa (Pennington et al. 2004; *Pseudosmodingium* and *Smodingium* were not part of the study). Recent phylogenetic analysis of 22 genera of Anacardiaceae using morphological, anatomical, and phytochemical data show *Pseudosmodingium* to be most closely related to *Astronium* Jacq. and *Schinopsis* Engl. (Aguilar-Ortigoza and Sosa 2004; *Cardenasiodendron* and *Loxopterygium* were not included in this study). A comprehensive phylogenetic analysis is necessary to understand generic relationships fully.

Despite previous phylogenetic and chemical studies in *Pseudosmodingium*, no taxonomic revision of the genus has been carried out. Therefore, a revision of the extant species of the genus is presented in this paper. It is based on both extensive field collections and the study of herbarium specimens.

KEY TO THE EXTANT SPECIES OF *PSEUDOSMODINGIUM*

1. Leaves with 13 or more leaflets; margin of leaflets serrate; panicles 4–10 cm long; flowers whitish, yellow at the base of the corolla; drupe pale . . . . . 1. *P. andrieuxii*
1. Leaves with less than 13 leaflets; margin of leaflets entire; panicles 15–38 cm long; flowers whitish; drupe gray or brown . . . . (2)
   2. Lateral leaflets petiolulate, petiolules 1–2.5 cm long; petals elliptic . . . . . 3. *P. perniciosum*
   2. Lateral leaflets sessile or subsessile, if subsessile the petiolules less than 1 cm long; petals ovate-elliptic or oblong . . . . (3)
      3. Base of leaflets truncate, not decurrent on the petiolule; panicles 25–38 cm long; anthers pyriform . . . 2. *P. barkleyi*
      3. Base of leaflets cuneate, decurrent on the petiolule; panicles 15–20 cm long; anthers globose . . . . . 4. *P. virletii*

TAXONOMIC TREATMENT

Pseudosmodingium Engl., Bot. Jahrb. Syst. 1: 419. 1881. LECTOTYPE here designated: *P. perniciosum* (Kunth) Engl., Bot. Jahrb. Syst. 1: 419. 1881.

Small trees, deciduous, dioecious or polygamo-dioecious, with thickened, dark-colored branches covered with tuberculate leaf scars;

bark papery, reddish brown. Leaves alternate, imparipinnate, clustered near the apices of the branches; leaflets several to many, glabrous to sparsely pubescent. Inflorescence an erect panicle, usually several panicles, clustered near the apex of the branch in the axils of leaves of previous years. Flowers small, on slender pedicels, bracts caducous, deltoid or lanceolate. Sepals 5, erect, glabrous, valvate; petals 5, spreading, imbricate and glabrous. Stamens 5, the filaments scarcely longer than the anthers, anthers globose to pyriform. Ovary 1-celled, winged; style 3-branched, terminal. Drupe flattened, winged, glabrous, exocarp lignified, mesocarp with resin canals, endocarp with four layers; fruit one-seeded; embryo accumbent, endosperm present, cotyledons slender.

A genus of six species, four extant and two fossil species endemic to Mexico, in dry forests or scrublands.

1. Pseudosmodingium andrieuxii (Baill.) Engl., Bot. Jahrb. Syst. 1: 420. 1881.

Smodingium andrieuxii Baill., Adansonia 11: 182. 1874. TYPE: MEXICO. 1834, *G. Andrieux 184* (HOLOTYPE: P; ISOTYPE: F! [fragment], photo at F!).

Pseudosmodingium multifolium Rose, Contr. U. S. Natl. Herb. 5: 143. 1897. TYPE: MEXICO. Oaxaca City, 6 Apr 1895, *E.W. Nelson 2542* (HOLOTYPE: US!; ISOTYPE: XAL!).

Shrubs or small trees; leaves imparipinnate, elliptic or lanceolate in outline, 10–20 cm long, petiole 1–5 (–6) cm, 13–27 leaflets, alternate to opposite, distance between leaflets ca. 1.5 cm, rachis slender; leaflets lanceolate, 1–4 (–5) cm long, 0.3–0.8 cm wide, chartaceous, pubescence of minute club-shaped glandular, simple and stellate trichomes above, glabrous below, except for a sparse pubescence on the main veins, apex acute to acuminate, base cuneate, margin serrate, venation craspedodromous, 12–18 secondary veins, leaflets subsessile, petiolule 0.1–0.5 cm, blade of leaflets dorsiventral, with monostratificate epidermis and stomata of 24–26 μm long, 17–19 μm wide. Inflorescence a panicle, 4–10 cm long, 3–4 cm wide, pedicels 0.3–0.5 cm long, slender; flowers whitish with a yellow center; sepals ovate, slightly imbricated, ca. 0.1 cm long, glabrous; petals oblong to ovate 0.2–0.3 cm long, 0.10–0.15 cm wide, glabrous; stamens barely shorter than the petals, filaments ca. 0.1 cm long, anthers botuliform or pyriform, ca. 0.1 cm long. Drupe broadly winged, oblate, polar diameter 0.6–0.9 cm, equatorial diameter 1.0–1.4 cm, glabrous, straw-colored.

Barkley and Reed (1940) recognized *Pseudosmodingium multifolium* as a different species from *P. andrieuxii*, based on the number of leaflets. However, our observations indicate that variation in the number of

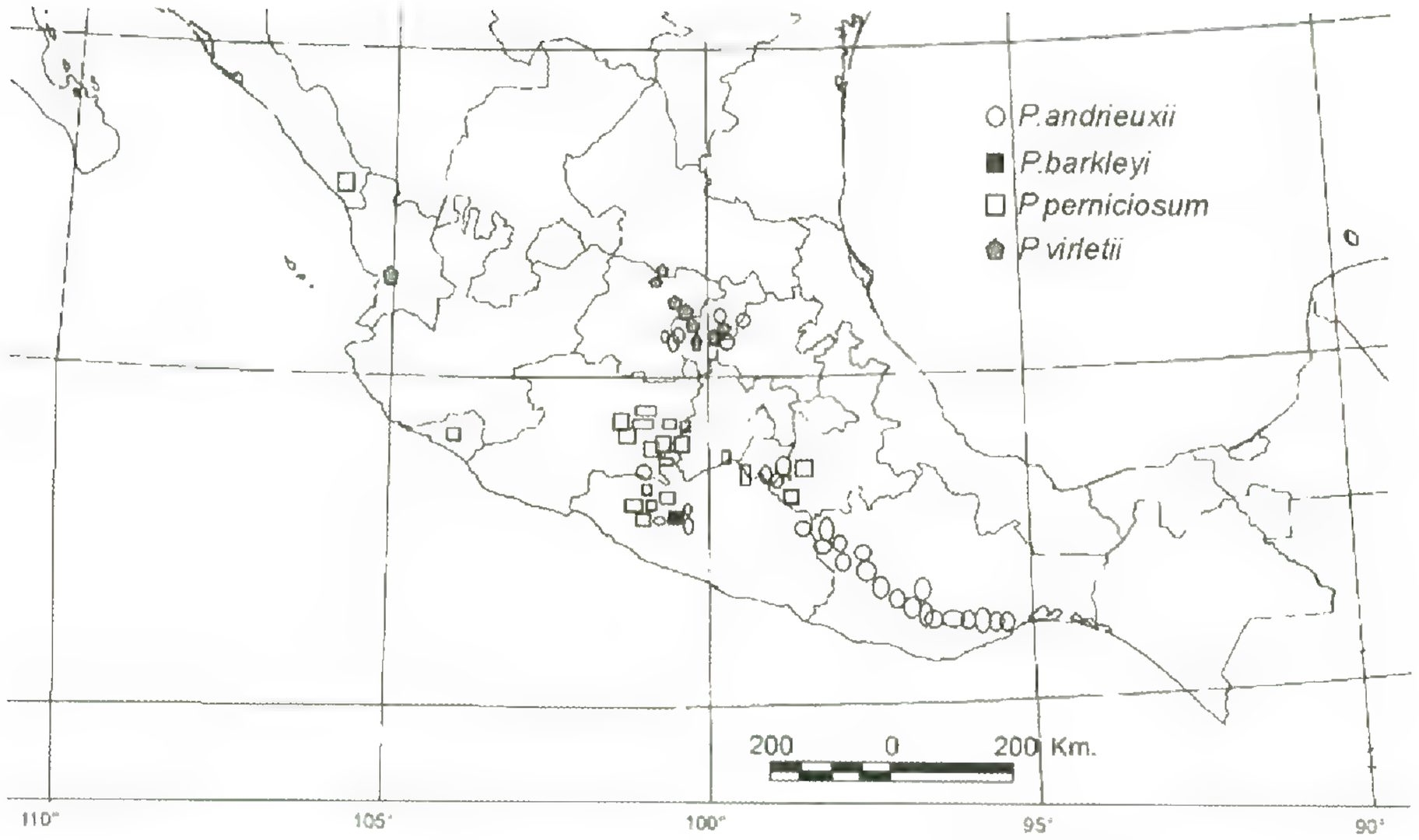

Figure 1. Distribution of *Pseudosmodingium* species. All sites lie between 15° and 25° N latitude.

leaflets is continuous. Furthermore, Aguilar-Ortigoza et al. (2004) in their phylogenetic study based on anatomical and morphological characters, found that both species were placed in the same subclade and that there were no autoapomorphic characters for these taxa. *Pseudosmodingium andrieuxii* is the most abundant and the most widely distributed species in the genus.

DISTRIBUTION, HABITAT, AND PHENOLOGY: *Pseudosmodingium andrieuxii* is found in central and southern Mexico, from San Luis Potosi to Oaxaca (Figure 1). The species is common in xerophytic habitats. It grows from 200 to 1900 m elevation. It flowers from March to May.

USES: This species is one the most toxic in the genus. Contact with leaves causes acute dermatitis. It is given common names such as "pirulillo" or "xhonguo" in otomí dialect.

SPECIMENS EXAMINED: MEXICO. Guerrero: Chilpancingo, Chilpancingo City, 4 Feb 1978, *M. Germán & F. Guevara 667* (FCME, MEXU); Eduardo Neri, Carrizal, 19 Feb 1995, *M. Luna 809* (FCME); Eduardo Neri, Casa Verde to Xochipala, 2 Feb 1965, *R. McVaugh 22189* (ENCB); Eduardo Neri, Zumpango del Rio, 11 Jun 1978, *M. Blanco et al. 290* (ENCB); Eduardo Neri, Km 15 S. Xochipala, 22 Mar 2000, *C. Aguilar 1207* (XAL); Iguala, Cañón de la Mano, 21 Dec 1978, *C. Catalán et al. 584* (CHAPA, IEB). Hidalgo: Izmiquilpan, May 1905, *C. Purpus 3168* (GH); Izmiquilpan, 1905, *J. Rose 8956* (US); Tecozautla, May 1914, *F. Salazar s.n.* (US); Zacualtipán, Rio Venados, 24 May 1985, *A. Espejo 1757* (IEB, UAMIZ); Zimapán, Barranca Tolimán, Apr 1947,

H. Moore 2585 (GH); Zimapán, Barranca Tolimán, Aug 1948, *H. Moore & C. Wood 4413* (GH); Zimapán, Rio San Juan, 6 Apr 1990, *A. Gómez 654* (IEB). Oaxaca: Carretera Oaxaca-Tehuantepec, Valle de la Ceiba, Mar 1949, *M. Carlson 1483* (F); Tlacolula, Totolapan, 23 Mar 1994, *S. Acosta 2417* (OAX); Tlacolula, Totolapan, 12 Mar 1986, *R. Torres 8217* (IEB, MEXU, XAL); Villa Alta, San Mateo Cajones, 12 May 1986, *R. Gereau & A. Moyer 168* (OAX); Cuicatlán, Cuesta de Quiotepec, 23 Apr 1919, *C. Conzatti 3556* (US); Ejutla de Crespo, Ejutla, 18 Feb 1985, *R. López et al. 318* (OAX); Etla, El Parian, Mar 1909, *C. Conzatti & I. Cancino 2435* (US); Huajuapan de León, Huajuapan, Aug 1963, *H. Gentry et al. 20296* (F); Huajuapan de León, La Reforma, Apr 1984, *R. Torres 4999* (XAL); Ixtlán, El Fortín, 14 Mar 1898, *C. Conzatti & V. González 669* (GH, MO); Ixtlan, Ixtlan to Ixtepeji, Apr 1983, *G.H. Martin 682* (MO); Ixtlan, Jalapa del Marquez, 26 Feb 1986, *C. Martínez 456* (MEXU); Juchitán, Guevea de Humboldt, 16 Mar 1983, *R. Torres 2537* (XAL); Matías Romero, La Puerta, 16 Feb 1982, *R. Torres 35* (MEXU, XAL); Miahuatlán, Valle de Oaxaca, 1841 1843, *F. Liebmann 259* (US); Miahuatlán, Cuixtlán, 18 Mar 1988, *R. Torres 11840* (IEB, MEXU, XAL); Nacaltepec, Cuesta de Ejutla, Jun 1895, *L. Smith 459* (GH); Oaxaca, Cerro del Tule, 31 Mar 1907, *C. Conzatti 1799* (F); Oaxaca, Monte Albán, Jun 1899, *J. Rose 4574* (US); Oaxaca, Oaxaca City, 6 Apr 1895, *E. Nelson 2542* (GH, US, XAL); San Lucas Quiavini, *s.d.*, *C. Robles 38* (OAX); San Carlos Yautepec, Tapanala, 28 Apr 1988, *S. Acosta 946* (IEB, OAX); San Carlos Yautepec, Tapanala, 6 Mar 1987, *A. Flores 1167* (IEB, OAX); Tamazulapan, Puente Río del Oro, 12 Apr 1987, *R. Torres 9599* (MEXU, XAL); Tehuantepec, Cerro Guingola, 15 Sep 1985, *L. Torres 171* (IEB, MEXU), 18 Mar 1987, *L. Torres 830* (IEB, MEXU); Tenango, Buenos Aires, 26 Mar 1984, *L. Torres 4793* (MEXU); Teotitlán del Camino, 15 Mar 1966, *C. Smith & N. Tejeda 4445* (US); Municipality Teotitlán del Camino, Apr 1978, *M. Sousa 9327* (MO); Zoquitlán, 1 Km SW Buenavista, 28 Apr 1988, *S. Acosta 945* (IEB, OAX); Río Yalalag, Apr 1919, *B. Reko 4154* (US). Puebla: Caltepec, Cerro Yaltepec, 12 Jan 1984, *P. Tenorio 5114* (XAL); Caltepec, El Tecomite, San Simón, Mar 1984, *P. Tenorio 5549* (MEXU); Matamoros, Amatitlán, Dec 1942, *F. Miranda 2509* (MEXU); Tehuacan, Tehuacán-Teotitlán del camino, Apr 1986, *O. Dorado & A. Salinas s.n.* (IEB, MEXU); Tehuacan, Tehuacan, Sep 1906, *J. Rose 11533* (US); San Luis Tultitlanapa, May–Jun 1908, *C. Purpus 3168* (F, GH, MO, NY); Zapotitlán de las Salinas, Salinas de Rinconada, 5 May 1979, *J. Calzada 5359* (XAL); Salinas de Rinconada, 7 Apr 1979, *F. Zavala 75* (XAL); Salinas de Rinconada, 4 May 1979, *J. Calzada 5341* (XAL). Queretaro: Cadereyta, Cañada de la culebra, 8 Jun 1993, *S. Zamudio 9511* (IEB); Cadereyta, Vizarrón, 1 May 1978, *S. Zamudio 2783* (IEB); San Joaquín, La Tinaja, 8 Mar 1996, *S. Zamudio 9765* (IEB, MEXU); Peñamiller, Peñamiller, 11 Apr 1977, *S. Zamudio 2030* (IEB); Peñamiller, 11 Apr 1977, *S. Zamudio 2034* (IEB); Peñamiller, 1 km north of Peñamiller, 13 Apr 1977, *S. Zamudio 2087* (IEB).

2. Pseudosmodingium barkleyi Miranda, Bol. Soc. Bot. México 26: 123. 1961. TYPE: MEXICO. Guerrero: Cañón del Zopilote, km. 246 carretera México–Acapulco, 15 Oct 1960, *A. Gómez-Pompa 390* (HOLOTYPE: MEXU!). Figure 2d, e.

Small trees, 3–5 m. Leaves imparipinnate, oblong in outline, (21–) 23–30 cm, petioles (6–) 8–11 (–13) cm long, (7–) 9–13 leaflets, distance between leaflets ca. 5 cm, rachis thick, striate and pubescent; leaflets oblong-ovate, 5–8 (–9) cm long, (3–) 5–8 cm wide, chartaceous to

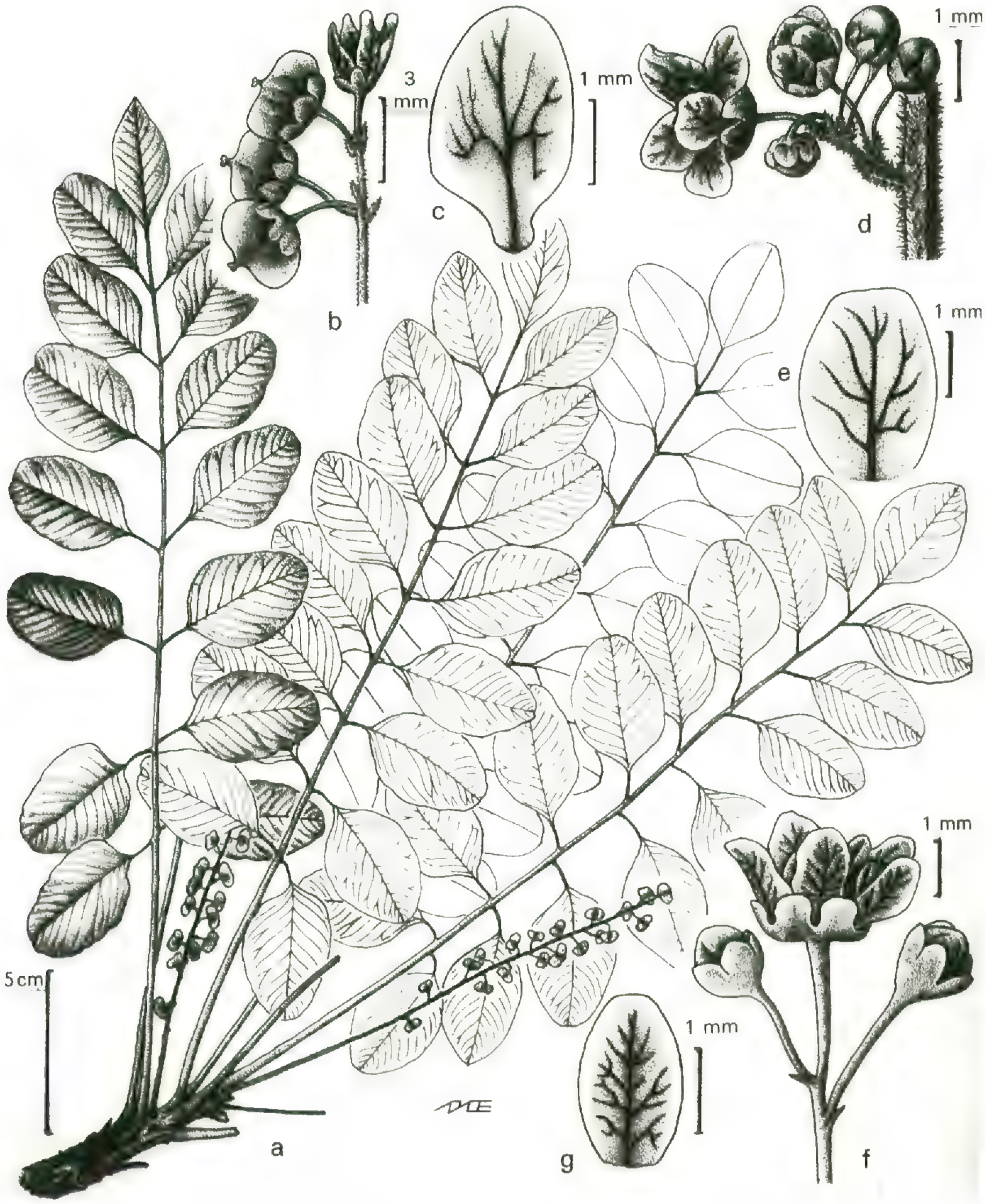

Figure 2. Morphological features of *Pseudosmodingium* species. a. Leaves and inflorescences of *P. perniciosum* (*Guerrero 776*). b. Branch with flower and fruit of *P. virletii* (*Zamudio 9655*). c. Petal of *P. virletii* (*Zamudio 9655*). d. Branch with flowers of *P. barkleyi* (*Aguilar 1199*). e. Petal of *P. barkleyi* (*Aguilar 1199*). f. Branch with flowers of *P. perniciosum* (*Guerrero 776*). g. Petal of *P. perniciosum* (*Guerrero 776*).

subcoriaceous, pubescence of simple and capitate trichomes, veins and margins whitened, margin entire, apex truncate-mucronate, base truncate to subcordate, base unequal, venation cladodromous, with 14 to 18 secondary veins, petiolules of lateral leaflets of 0.1–0.3 cm, petiolule of

terminal leaflet 0.2–0.4 cm, blade of leaflets dorsiventral with monostratificate epidermis and stomata of 24–28 μm long, 18–19 μm wide. Inflorescence a panicle, 25–38 cm long, 7–12 cm wide, 28–30 branches, 25–45 flowers in basal branches, pedicels 0.2–0.4 cm long, slender; flowers whitish, sepals imbricate, suborbicular to deltoid, 0.4–0.7 cm long, petals ovate-elliptic ca. 0.2 cm long, ca. 0.1 cm wide, glabrous; filaments 0.07–0.1 cm long, anther pyriform, 0.05–0.08 cm. Fruit a drupe, broadly winged, oblate, polar diameter 0.6–0.8 cm, equatorial diameter 0.9–1 cm, glabrous, grayish.

Pseudosmodingium barkleyi is the species with the most restricted distribution, having been collected in only a few locations in the area of Cañon del Zopilote.

DISTRIBUTION, HABITAT, AND PHENOLOGY: Endemic to Guerrero, Mexico (Figure 1). This species grows in tropical dry forests on karstic soils. It flowers from April to August.

USES: As with all *Pseudosmodingium* species, contact with leaves and bark of *P. barkleyi* produces dermatitis. It is known locally as "cuajiote" or "tetlate."

SPECIMENS EXAMINED: MEXICO. Guerrero: Cañon del Zopilote, road to Xochipala, Eduardo Neri, Mar 2000, *C. Aguilar 1199* (XAL); Cañon del Zopilote, 31 May 1980, *A. González s.n.* (FCME); Km 14 carretera Mezcala–Chilpancingo, 15 Jul 1981, *R. Fonseca 175* (FCME, MEXU); Km 3 carretera Tlalcozotitlan–Copalillo, 7 Aug 1982, *R. Fonseca 407* (FCME); NW Huamuchtitlan, 5 Aug 1982, *R. Fonseca 399* (FCME); Km 5.5 NW de Mezcala, 3 Jul 1980, *J. Contreras 404* (FCME); 2 km W Huitzuco, 3 Oct 1981, *G.H. López & H. Gutiérrez 49* (FCME).

3. Pseudosmodingium perniciosum (Kunth) Engl., Bot. Jahrb. Syst. 1: 420. 1881. Figure 2a, f, g.

Rhus perniciosa Humb., Bonpl. & Kunth, Nov. Gen. Sp. 7: 10. 1825. TYPE: MEXICO. Guerrero: Tepecuacuilco, *s.d., A. von Humboldt & A. Bonpland 3955* (HOLOTYPE: P, photo at P!).

Rhus pterocarpus DC., Prodr. 2. 84. 1825. TYPE: MEXICO. 1787–1804, *M. Sessé, J.M. Mociño, J.D. del Castillo & J. Maldonado 4938* (HOLOTYPE: F! [fragment], photo at F!).

Spathelia (?) rhoifolia DC., Prodr. 2. 84. 1825, in part.

Pseudosmodingium pterocarpus (Sessé & Moc.) F.A. Barkley, Ann. Missouri Bot. Gard. 24: 263. 1937.

Pseudosmodingium rhoifolium (DC.) F.A. Barkley, Ann. Missouri Bot. Gard. 24: 500. 1937.

Rhus pterocarpus Sessé & Moc., Pl. Nov. Hisp., p. 47. 1888, in part.

Trees, 4–10 m; leaves imparipinnate, oblong in outline, (22–) 25–36 (–40) cm long, 10–20 cm wide, petiole (5.5–) 8–13 cm long, 9–15 leaflets, distance between leaflets ca. 4 cm, rachis coarse, glabrous, leaflets obovate to rhombic-ovate, 3.5–7 cm long, 1.5–5 cm broad, coriaceous, glaucous, glabrous to a sparse pubescence of simple trichomes, veins and margins whitened, margin entire, apex truncate to subacute, sometimes mucronate, base cuneate, decurrent to the petiolule, base unequal, venation cladodromous, with 18–22 secondary veins, lateral petiolules 1.5–2.5 cm long, terminal petiolule 3–4.5 cm, blade of leaflets dorsiventral with monostratificate epidermis and several giant stomata of 32–38 μm long, 19–25 μm wide. Inflorescence a panicle 15–35 (–38) cm long, 7–10 cm broad, (10–) 15–22 (–24) branches, 10–38 (–45) flowers on basal branches, pedicels 0.4–0.5 cm long, slender; flowers whitish, sepals slightly imbricate, suborbicular to deltoid, ca. 0.1 cm long, petals elliptic ca. 0.2 cm long, ca. 0.12 cm wide, glabrous; filaments 0.07–0.1 cm, anthers globose, 0.05–0.1 cm. Fruit a drupe, broadly winged, oblate, polar diameter 0.6–0.8 cm, equatorial diameter 0.9–1.2 cm, glabrous, brown.

This species displays a great variation in leaflet shape, which causes problems in species recognition. We here include as synonyms *Pseudosmodingium rhoifolium* and *P. pterocarpus*. Barkley (1937), when transferring *Rhus pterocarpus* to *Pseudosmodingium*, mentioned that *P. pterocarpus* was very similar to *P. perniciosum*. Furthermore, when Barkley transferred *Spathelia rhoifolia* to *P. rhoifolium*, he considered that it was the same species as *P. pterocarpus*. Based on the principle of priority, the name should be *P. rhoifolium*. Aguilar et al. (2004) included *P. rhoifolium* as a terminal taxon in their morphology-based phylogenetic study. Its placement was problematic because it was known only from the type specimen and the only characters available were leaf characters. However, the position of *P. rhoifolium* was in the same clade as *P. perniciosum*. The epithet refers to the toxicity of the leaves and bark, contact with which can cause severe dermatitis.

DISTRIBUTION, HABITAT, AND PHENOLOGY: Endemic to Mexico, mostly on the western slopes of the Pacific mountains (Figure 1). *Pseudosmodingium perniciosum* is found in tropical dry forests, on limestone soils, from 700 to 1500 m. It flowers from May to September.

USES: This is the most toxic species of the genus. In Guerrero, the leaves are crushed and used to heal wounds. It bears local names such as "cuajiote colorado" and "hincha huevos."

SPECIMENS EXAMINED: MEXICO. Colima: Comala, El Terrero, 31 Jan 1987, *R. Cuevas & M. Rosales 1765* (IEB). Guerrero: District Mina, Placeres-Cigarrillo, 31 Nov 1936, *G.H. Hinton 9794* (GH); Achotla, N of Rio Balsas, 16 Nov 1937, *Y. Mexía 8824* (F, GH); Ahuacoutzingo, Trapiche viejo Km 40 a Chilapa, 8 Oct 1982, *S. Acosta & R. López 72* (IEB, XAL); Coyuca, Chacamerito, 8 Nov 1934, *G.H. Hinton 6946* (F, GH); Coyuca, Chirapitiro, 26 Oct 1934, *G.H. Hinton 6868* (F); Coyuca, Pungarabato, 11 Jun 1934, *G.H. Hinton 6939* (GH); Cacahuamilpa, Rio Chontalcoatlán, 4 Oct 1964, *L. González 747* (F); Eduardo Neri, Km. 12 N of Zumpango, 16 Sep 1994, *J. Calónico 1249* (FCME); Iguala, Cañon de la mano, 26 Oct 1986, *C. Catalán 387* (IEB); Iguala, Montañas above Iguala, 5 Oct 1900, *C. Pringle 8385* (F, GH); Taxco, 7 Oct 1958, *F. Cox 1873* (XAL); Zirandaro, Km. 22 S Zirandaro, Apr 1970, *G. Tellez s.n.* (FCME). State of Mexico: Barranca de los Muñecos, Tejupilco, 14 Sep 1999, *C. Aguilar 1197* (XAL); Bejucos, Tejupilco, District Temascaltepec, 11 Nov 1933, *G.H. Hinton 5198* (GH); Bejucos-Palmar Chico, Tejupilco, Apr 1981, *I. García 131* (CODAGEM); Cerro de Nanchititla, Tejupilco, 8 Sep 1954, *E. Matuda et al. 31590* (CODAGEM, MEXU); El Salto de Nanchititla, 600 m, Sep 1990, *C. Aguilar 107* (CODAGEM); 38 km. S of Mexico City, Jul 1940, *C. Hitchcock & L. Stafford 7052* (GH); District Temascaltepec, Ocotepec, 24 Nov 1934, *G. Hinton 7034* (F, GH, NY, XAL); Naranjo, District Temascaltepec, May 1932, *G. Hinton 1993* (GH, NY). Michoacan: Apatzingan, Aguililla, Sep 1939, *G. Hinton 15300* (GH); Apatzingan, 20 Aug 1941, *W. Leavenworth & H. Hoogstraal 1710* (F, XAL); Apatzingan, 22 Aug 1941, *W. Leavenworth & H. Hoogstraal 1757* (F, GH); Aquila, Cerro Ojo de Agua, 2 Apr 1980, *B. Guerrero 776* (XAL); Arteaga, 8 Dec 1977, *J. Cházaro 753* (XAL); El Zopilote, Mar 1903, *E. Nelson 6976* (GH, MO, US). Morelos: Alpuyeca, 7 km a las Grutas, 24 Oct 1983, *S. Acosta 1983* (XAL); Cuernavaca, near Xochicalco, 18 Jul 1938, *L. Kenoyer 651* (F); Cuernavaca, Cuernavaca, 1905, *J. Lemmon 194* (F, GH, MO); Miacatlán, Cerro las Cantinas, 3 Nov 1981, *A. Monroy 1690* (XAL); Tepalcingo, El Limón, 19 Nov 1980, *R. Ortega 1561* (XAL); Tepalcingo El Limón, Tepalcingo, 19 Nov 1980, *A. Guerrero 1332* (IEB); Yautepec, 3 km. E of Amador Salazar, Nov 1984, *M. Ishiki 984* (IEB). Nayarit: Tepic, Volcán Ceboruco, 26 Sep 1995, *J. Cházaro 7584* (XAL). Puebla: Jolalpan, San Pedro de las Palmas, 9 Jul 1990, *R. Razo & R. García 111-38* (IEB); Zapotitlan, Santa Ana Teloxtoc, 4 Apr 1979, *F. Zavala et al. 1670* (XAL). Sinaloa: Culiacán, Bagracitos, 9 Dec 1982, *P. Tenorio 3016* (IEB); Culiacán, Meza Malqueson, cerro Colorado, 8 Dec 1939, *H.S. Gentry 5173* (GH).

4. Pseudosmodingium virletii (Baill.) Engl., Bot. Jahrb. Syst. 1: 420. 1881. Figure 2b, c.

Smodingium virletii Baill., Adansonia 11: 182. 1874. TYPE: MEXICO. Province of San Luis: 1851, *V. d'Aoust 1044* (HOLOTYPE: P, photo at F!).

Small trees or shrubs, 2–4 m; leaves oblong in outline, 20–23.5 cm long, petiole 5–10 cm long, (9–) 11–13 (–15) leaflets, distance between leaflets ca. 2.2 cm, rachis thick, glabrous, leaflets oblong to obovate, 3–5 (–6) cm long, (1–) 2–3 cm wide, coriaceous, glaucous, cerose, glabrous or with a sparse pubescence of simple and stellate trichomes, sometimes orange-colored, margin entire, apex truncate-emarginate, base cuneate, decurrent on the petiolule, venation cladodromous, with 18–20

secondary veins, lateral petiolules 0.3 cm long, terminal petiolule 1.5 cm, blade of leaflets isobilateral with polystratified and small sunken stomata of 14–18 μm long, 9–17 μm wide. Inflorescence a panicle, (13–) 15–20 (–25) cm long, 5–10 (–12) cm wide, 14–22 branches, (18–) 20–40 (–45) flowers in basal branches, pedicels 0.6–0.7 cm long, slender; flowers whitish, sepals slightly imbricate, ovate ca. 0.1 cm long, petals oblong, whitish, venose, ca. 0.2 cm long, ca. 0.12 cm wide, glabrous; filaments 0.1 cm, anthers globose 0.05–0.1 cm. Fruit a drupe, broadly winged, oblate, polar diameter 0.6–0.7 cm, equatorial diameter 1.0–1.3 cm, glabrous, brown.

Rzedowski and Calderón (1999) reported hybrids between *Pseudosmodingium andrieuxii* and *P. virletii* in the "El Bajio" area. The two species grow sympatrically in some localities and some plants have the number, pubescence, and shape of leaflets of *P. andrieuxii*. They have 13 leaflets, with an acute apex, and the same pubescence. However, the texture and color of the pubescence of the leaflets are similar to those of *P. virletii*. The authors mentioned that the putative hybrids produced flowers and fruits. They come from Cadereyta in Queretaro, which is part of "El Bajio." We also observed these characters [*S. Zamudio & E. Pérez 9510* (IEB); *S. Zamudio 3556* (IEB)].

DISTRIBUTION AND HABITAT: Endemic to the central area of Mexico (Figure 1). *Pseudosmodingium virletii* grows in xerophytic scrublands and in dry tropical forests at elevations between 700–1500 m.

USES: The small trees are planted as fences mainly in pasturelands; the toxic catechols prevent cattle from crossing these fences. This species is given common names such as "chichote," "guau," and "xhangua," the two last names in otomí dialect.

SPECIMENS EXAMINED: MEXICO. Hidalgo: Jacala, Barranca Seca, Jacala to Pacula, 29 Apr 1947, *H. Moore 2743* (GH). Guanajuato: Xichú, Mina la Aurora, 30 Oct 1986, *J. Rzedowski 41486* (IEB). Queretaro: Arroyo Seco, to Jalpan de Serra, 29 Mar 2000, *C. Aguilar 1204* (XAL); San Joaquín, Cañada de la Culebra, 18 Nov 1978, *S. Zamudio 3556* (IEB); Cadereyta, Cañada de la Culebra, 8 Jun 1995, *S. Zamudio & E. Pérez 9510* (IEB); Ayutla, 2 km. N road Jalpan-Rio Verde, 28 Mar 1984, *A. García & L. Vargas 1379* (MEXU, XAL); Jalpan de Serra, Río Estorax Canion, 5 Mar 1996, *S. Zamudio 9655* (IEB); Landa de Matamoros, Puerto Blanco, 13 Mar 1988, *A. Herrera 107* (IEB); Municipality Cadereyta, La Tinaja, 8 Jul 1995, *S. Zamudio 9510* (IEB).

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NEW ENGLAND NOTE

FLORAS OF PEQUAWKET AND HEATH POND BOGS, OSSIPEE, NEW HAMPSHIRE

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Pequawket Bog and Heath Pond Bog are located in the Town of Ossipee, near the town line, in Carroll County, New Hampshire. Although the two sites lie approximately one mile apart (Figure 1), the floristic and vegetational differences exhibited by each peatland are striking.

Pequawket Bog, situated between Long Sands Road and Pequawket Trail, off State Route 25, is a peatland of approximately 9.9 hectares (24.4) acres, including a 2.8 hectare (7 acre) pond. The peatland complex has a large sedge meadow, dominated by *Carex lasiocarpa*, on the northwest side of the pond, while the east, south, and west sides have a more typical bog flora, with a deep sphagnum mat and low ericaceous shrubs. A detailed site description and vegetation analysis are provided elsewhere (Fahey 1993; Fahey and Crow 1995).

Heath Pond Bog, located approximately 2 miles northeast of the village of Center Ossipee, along State Route 25, is a peatland of approximately 16.2 hectares (40 acres), including a 2-hectare (5-acre) pond. The floating mat around the pond is, on average, approximately 3 m wide. Immediately around the floating mat, and on the extensive mat west of the pond, ericaceous shrubs and scattered *Picea mariana* and *Larix laricina* of dwarfed stature dominate. Further site information and description of the flora and vegetation are given elsewhere (Fahey 1993).

Heath Pond Bog has been a point of interest to professional and amateur botanists for many years, and as a result of their efforts, the site was designated a National Natural Landmark in July, 1972. While it was regarded as a "classic example of bog succession" containing a "greater variety of plants than known in any other peat bog in the state" (Steele, in Lyon and Reiners 1972, p. 61), our study has revealed that nearby Pequawket Bog, apparently unknown to Steele and colleagues, has even greater species diversity.

As part of a detailed study of the flora and vegetation of Pequawket and Heath Pond Bogs during the summer of 1991, total inventories of

Figure 1. Aerial photograph of Pequawket Bog (lower right), and Heath Pond Bog (far upper left), looking westward.

the vascular plant species found in the two peatlands were carried out (Fahey 1993; Fahey and Crow 1995); numerous additional visits to the peatlands have occurred annually. During the growing season the sites were visited no less than once a week. Nomenclature follows Crow and Hellquist (2000a, b) and Gleason and Cronquist (1991).

The vascular flora of Pequawket Bog consists of 44 families, 80 genera, and 109 species; 5 pteridophytes, 4 gymnosperms, and 100 angiosperms (53 dicots and 47 monocots). The predominant families are the Cyperaceae (21 species; 19.3% of total flora) and the Ericaceae (11 species; 10.0% of total flora).

The vascular flora of Heath Pond Bog consists of 26 families, 47 genera, and 72 species; 2 pteridophytes, 4 gymnosperms, and 66 angiosperms (35 dicots and 31 monocots). Three species (*Arethusa bulbosa*, *Carex pauciflora*, *Platanthera blephariglottis*) have been documented by herbarium specimens in the past, but were not seen during the summer of 1991 nor in subsequent annual visits. One species (*Arceuthobium pusillum*) was added to the flora in 1994. The predominant families are the Cyperaceae (20 species; 28.2% of total flora) and the Ericaceae (12 species; 18.3% of total flora).

In order to compare floristic similarities between the two peatlands, a Sørensen Index of Similarity was calculated. This method of data analysis uses the number of species shared between two sites (c), and the total number of species for each of the two sites in question (a and b) to determine the similarity of the two floras with respect to species composition (Mueller-Dombois and Ellenberg 1974). Sørensen's Index is calculated as follows:

$$SI = [2c \div (a + b)] \times 100$$

The Sørensen Similarity Index (SI) provides a value that represents the percentage of species in common between the two floras (Mueller-Dombois and Ellenberg, 1974). According to Barbour et al. (1987), in comparing any two plant communities, a similarity index greater than 50% would indicate strong similarity and the two communities could be viewed as representing the same association. Pequawket Bog and Heath Pond Bog have 58 species in common, giving a Sørensen Similarity Index value of 64.08%. For perspective, C. Eric Hellquist's (1994) comparison of floristic similarity among several New Hampshire bogs revealed a similar value between the bog he studied in Moultonborough and Pequawket Bog (SI = 64.4%), but a lower value between the Moultonborough bog and Heath Pond Bog (SI = 49.5%). The highest percentage of similarity Hellquist noted was between Pequawket Bog and a bog in Hillsborough,

New Hampshire studied by Debra Dunlop (1987), with an SI value of 75.2%. Both bogs had a much lower similarity index with a bog studied by Crow (1969) in Michigan (Pequawket Bog, SI = 45.0%; Heath Pond Bog, SI = 29.9%). These values reflect the complex nature of factors affecting the floristic makeup of peatland vegetation—factors such as differences in basin morphology, hydrology, nutrient regimes, local topography, and floristic composition of the vegetation of the area.

The floras of the two peatlands are presented in Table 1. The checklists are presented in this format to allow botanists and students visiting these two sites to compare species present in each of the bogs.

The current *Plant Tracking List* of the New Hampshire Natural Heritage Bureau (2003) was consulted to determine if any of these species had special protected status in the state. Several plants occurring in the peatlands are noteworthy. *Eriophorum angustifolium*, an endangered species for New Hampshire, was first reported for the state from Heath Pond Bog in 1984 (Brackley and Crow 1989). This species was also found in Pequawket Bog during this study, and its presence represents a second station for this species in the state of New Hampshire. *Arethusa bulbosa*, documented from Heath Pond Bog by a voucher specimen dated June 29, 1937, at the University of New Hampshire (NHA; acc. no. 74765—no collector indicated, but from collection given to NHA by Frederic Steele), but not documented from there since, also has "Endangered" status in New Hampshire. A second herbarium sheet (NHA; acc. no. 81316) has a handwritten note in Frederic Steele's hand, noting that he had checked Heath Pond Bog on June 16 and 23, 1971, but found no plants of this species. Brumback and Mehrhoff, et al. (1996) have listed *A. bulbosa* in *Flora Conservanda*, the list compiled by New England Plant Conservation Program (NEPCoP), noting that this orchid is in decline in Connecticut, Massachusetts, Rhode Island, and Vermont. Other plants included on the current *Plant Tracking List* of the New Hampshire Natural Heritage Bureau (2003) present in both peatlands include *Calopogon tuberosa*, *Platanthera blephariglottis*, *Pogonia ophioglossoides*, and *Sarracenia purpurea*. These four species are listed as "Special Concern" status. One additional species, *Potamogeton confervoides*, is listed as "State Watch" status on an unpublished list of plants that have the potential of being raised to the unofficial status category "protected" by the New Hampshire Natural Heritage Bureau; it is also listed in *Flora Conservanda* (Brumback and Mehrhoff 1996).

Table 1. The floras of Pequawket and Heath Pond Bogs (historical records indicated as H). Voucher specimens are cited in Fahey (1993) and housed in NHA.

Species	Pequawket Bog	Heath Pond Bog
Acer rubrum L.	X	X
Alnus incana subsp. *rugosa* (Du Roi) Clausen	X	
Amelanchier canadensis (L.) Medik.	X	X
Andromeda glaucophylla Link	X	X
Apios americana Medik.	X	
Arceuthobium pusillum Peck		X
Arethusa bulbosa L.		H
Aronia melanocarpa (Michx.) Elliott	X	X
Aster nemoralis Aiton	X	
Betula populifolia Marshall	X	X
Bidens cernua L.	X	
Brasenia schreberi J.F. Gmel.	X	
Calamagrostis canadensis (Michx.) P. Beauv.	X	
Calla palustris L.	X	
Calopogon tuberosus (L.) Britton, Sterns & Poggenb.	X	X
Carex atlantica Bailey subsp. *atlantica*		X
Carex atlantica subsp. *capillacea* (Bailey) Reznicek	X	
Carex canescens L.	X	X
Carex crinita Lam. var. *crinita*	X	
Carex echinata Murray	X	
Carex folliculata L. var. *folliculata*	X	X
Carex gynandra Schwein.		X
Carex lasiocarpa var. *americana* Fernald	X	
Carex limosa L.		X
Carex lurida Wahlenb.		X
Carex oligosperma Michx.	X	X
Carex pauciflora Lightf.		H
Carex scoparia Schkuhr *ex* Willd.	X	X
Carex stricta var. *strictior* (Dewey) Carey	X	X
Carex trisperma Dewey	X	X
Carex utriculata Boott	X	
Carex vesicaria L.		X
Cephalanthus occidentalis L. var. *occidentalis*	X	
Chamaedaphne calyculata (L.) Moench	X	X
Cladium mariscoides (Muhl.) Torr.	X	X
Coptis trifolia var. *groenlandica* (Oeder) Fassett		X
Cornus stolonifera Michx.	X	
Dalibarda repens L.	X	
Decodon verticillatus (L.) Elliott	X	X
Drosera intermedia Hayne	X	X
Drosera rotundifolia L.	X	X
Dulichium arundinaceum (L.) Britton	X	X
Eleocharis robbinsii Oakes	X	
Eleocharis smallii Britton	X	

Table 1. Continued.

Species	Pequawket Bog	Heath Pond Bog
Eriocaulon aquaticum (Hill) Druce	X	
Eriophorum angustifolium Honck.	X	X
Eriophorum tenellum Nutt.	X	
Eriophorum vaginatum subsp. *spissum* (Fernald) Hultén	X	X
Eriophorum virginicum L.	X	X
Euthamia graminifolia (L.) Nutt. *ex* Cass. var. *graminifolia*	X	
Galium trifidum L.	X	
Gaultheria procumbens L.	X	X
Gaylussacia baccata (Wangenh.) K. Koch	X	X
Glyceria canadensis (Michx.) Trin.	X	X
Ilex verticillata (L.) A. Gray	X	X
Iris versicolor L.	X	X
Juncus canadensis J. Gay	X	
Juncus effusus L.	X	X
Juncus pelocarpus E. Mey.	X	
Kalmia angustifolia L.	X	X
Kalmia polifolia Wangenh. subsp. *polifolia*	X	X
Larix laricina (Du Roi) K. Koch	X	X
Ledum groenlandicum Oeder		X
Leersia oryzoides (L.) Sw. var. *oryzoides*	X	
Lycopus uniflorus Michx.	X	
Lyonia ligustrina (L.) DC. var. *ligustrina*	X	X
Lysimachia terrestris (L.) Britton, Sterns & Poggenb.	X	X
Maianthemum canadense Desf. var. *canadense*	X	
Menyanthes trifoliata var. *minor* Raf.	X	
Mitchella repens L.		X
Myrica gale L.	X	
Nemopanthus mucronata (L.) Trel.	X	X
Nuphar variegata Engelm. *ex* Durand	X	X
Nymphaea odorata Aiton subsp. *odorata*	X	
Nymphoides cordata (Elliott) Fernald	X	X
Onoclea sensibilis L.	X	
Osmunda cinnamomea L.	X	X
Osmunda regalis var. *spectabilis* (Willd.) A. Gray	X	
Peltandra virginica (L.) Schott & Endl.	X	X
Picea mariana (Mill.) Britton, Sterns & Poggenb.	X	X
Pinus rigida Mill.	X	X
Pinus strobus L.	X	X
Platanthera blephariglottis (Willd.) Lindl.	X	H
Pogonia ophioglossoides (L.) Ker-Gawl.	X	X
Pontederia cordata L.	X	
Potamogeton amplifolius Tuck.	X	
Potamogeton confervoides Rchb.	X	
Potamogeton epihydrus var. *ramosus* (Peck) House	X	
Potamogeton natans L.	X	

Table 1. Continued.

Species	Pequawket Bog	Heath Pond Bog
Potamogeton oakesianus J.W. Robbins	X	
Rhododendron canadense (L.) Torr.	X	X
Rhynchospora alba (L.) Vahl	X	X
Rosa nitida Willd.	X	
Rubus hispidus L.	X	X
Sagittaria latifolia Willd.	X	
Salix discolor Muhl.	X	
Sarracenia purpurea L.	X	X
Scheuchzeria palustris subsp. *americana* (Fernald) Hultén	X	
Scirpus cyperinus (L.) Kunth	X	X
Scirpus microcarpus J. Presl & C. Presl		X
Smilacina trifolia (L.) Desf.	X	X
Sparganium americanum Nutt.	X	
Spiraea latifolia (Aiton) Borkh.	X	X
Spiraea tomentosa L.	X	
Symplocarpus foetidus (L.) Nutt.	X	X
Thelypteris palustris var. *pubescens* (Lawson) Fernald	X	
Toxicodendron vernix (L.) Kuntze	X	
Triadenum virginicum (L.) Raf.	X	X
Trientalis borealis Raf.	X	
Utricularia cornuta Michx.	X	X
Utricularia geminiscapa Benj.		X
Utricularia intermedia Hayne	X	
Utricularia purpurea Walter	X	
Utricularia vulgaris subsp. *macrorhiza* (LeConte) Clausen	X	
Vaccinium corymbosum L.	X	X
Vaccinium macrocarpon Aiton	X	X
Vaccinium myrtilloides Aiton		X
Vaccinium oxycoccos L.	X	X
Viburnum cassinoides L.	X	X
Viburnum recognitum Fernald	X	
Viola macloskeyi subsp. *pallens* (Banks *ex* DC.) M.S. Baker	X	
Woodwardia virginica (L.) Sm.	X	X
Xyris montana Ries	X	X
TOTAL	109	72
SHARED SPECIES: 58		

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NOTE

LECTOTYPIFICATION OF THE NAME *GENTIANA QUINQUEFOLIA* VAR. *OCCIDENTALIS* (GENTIANACEAE)

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Gentiana quinquefolia ["*quinqueflora*"] var. *occidentalis* A. Gray is the basionym of the currently used name *Gentianella quinquefolia* subsp. *occidentalis* (A. Gray) J.M. Gillett. Gillett (1957, 1963) considered this name to have been based on plate 3496 in *Curtis's Botanical Magazine* and the accompanying description of *Gentiana quinqueflora* [*sic*] by Robert Graham (Hooker 1836). However, when Gray (1848) published the name in the first edition of his *Manual*, he did not mention that plate or description. He first equated the representation of *G. quinqueflora* in the *Botanical Magazine* with his var. *occidentalis* in the *Synoptical Flora* (1878). Even then, the plate was equated "mainly" with var. *occidentalis*. There was no indication that this plate and description had been the basis of the description published by Gray 30 years earlier.

According to Hooker (1836), the plate was prepared from a drawing sent to him by Charles Wilkins Short of Lexington, Kentucky. Short's specimens of this species, cited below, represent subsp. *occidentalis*. The accompanying description by Graham was based largely or entirely on plants raised, presumably by or on behalf of Graham, from seeds sent to England from New York and from herbarium specimens collected by Heinrich Karl Beyrich at the Peaks of Otter in the Blue Ridge Mountains of Virginia. The supplementary illustrations, showing floral details, were drawn from the cultivated plants. The only subspecies occurring either in New York or in Virginia is subsp. *quinquefolia*.

At NY, two collections mounted on one sheet, *ex* herb. John Torrey, have been designated possible types of the name *Gentiana quinquefolia* var. *occidentalis* A. Gray. The plant on the left, collected by William Cullen Bryant at Cummington, Massachusetts, represents subsp. *quinquefolia* and was so annotated by John M. Gillett. Its provenance precludes its being of nomenclatural significance in the present context. The stems in the center and right, collected by John Leonard Riddell at

Worthington, Ohio, represent subsp. *occidentalis* and were so annotated by Gillett. They may have been seen by Gray prior to 1848, but they were neither annotated by him nor mentioned in any of his publications. At OS, a specimen of subsp. *occidentalis ex* herb. John M. Coulter, collected at New Albany, Indiana, by Asahel Clapp in 1837 has been considered a type, but no specimen collected by Clapp was cited by Gray and there is no evidence that he saw any replicate of that collection.

To eliminate uncertainty as to the correct application of the epithet *occidentalis*, it is appropriate to designate as lectotype a specimen that was in Gray's possession when he wrote the first edition of his *Manual* and was identified as var. *occidentalis* by him. Such a specimen is among those from Gray's own herbarium now at GH. It was collected by Short in Kentucky and bears Gray's label with the printed designation of its distribution as "Western States," corresponding to the range of the taxon as given in the *Manual*. Although the wording in the *Manual*, "through the Western States," implies that Gray had already seen more than one specimen of this taxon, no other specimen from Gray's herbarium bears such a label. The designation of this specimen as the lectotype maintains the use of the epithet *occidentalis* in its established sense.

Gentianella quinquefolia subsp. occidentalis (A. Gray) J.M. Gillett, Ann. Missouri Bot. Gard. 44: 245. 1957; *Gentiana quinquefolia* ["*quinqueflora*"] var. *occidentalis* A. Gray, Manual, ed. 1, 359. 1848, basionym. *Gentianella quinquefolia* var. *occidentalis* (A. Gray) Small, Fl. S.E. U.S., ed. 1, 929. 1903; *Amarella occidentalis* (A. Gray) Greene, Leafl. Bot. Observ. Crit. 1: 53. 1904; *Aloitis occidentalis* (A. Gray) Greene, Leafl. Bot. Observ. Crit. 1: 94. 1904; *Gentiana occidentalis* (A. Gray) T.J. Fitzp., Iowa Naturalist 2: 13. 1906, *non* Jakow. 1899; *Gentianella occidentalis* (A. Gray) Small, Man. S.E. Fl. 1052. 1933; *Aloitis quinquefolia* subsp. *occidentalis* (A. Gray) Á. Löve & D. Löve, Taxon 34: 164. 1985. LECTOTYPE here designated: U.S.A. Kentucky: Barrens [not more precisely located], *C.W. Short s.n., s.d.* (LECTOTYPE: GH!; ISOLECTOTYPE: K!).

ACKNOWLEDGMENTS. I thank Jeffrey Morawetz of The Ohio State University for sending images of the specimen from Indiana and its label. I am also grateful to Emily Wood et al. for opportunities to study specimens at GH, and to those at NY who provided images of nomenclaturally significant specimens on the Internet. This paper is Contribution No. 121 from the Royal Botanical Gardens, Hamilton, Ontario, Canada.

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NOTE

NOTES ON THE BOX HUCKLEBERRY, *GAYLUSSACIA BRACHYCERA* (ERICACEAE), AND ITS UNEXPECTED PRESENCE IN NORTH CAROLINA

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The box huckleberry, *Gaylussacia brachycera* (Michx.) A. Gray, is now known in northern Durham County, North Carolina. This is the first record for the state, extending its range approximately 160 miles southeastward from western Virginia. The chronology of discovery of this remarkable species is outlined below, and its continued unsettled systematic position is noted, two centuries after its initial publication by Michaux (1803). The North Carolina occurrence of this species, which is thought to have been a long-time resident of this region and not a recent introduction, strongly suggests that floristics currently remains an important challenge to both professional and amateur naturalists and that their future close cooperation is essential to advancing the floristic inventory of much of our area, as well as much of the nation. As Wilson (2000) has emphatically pointed out, floristic and faunistic work remains both scientifically exceedingly important and urgent for the welfare of mankind. The immediate stimulus for these notes on the box huckleberry was its recent discovery for the first time in North Carolina by Stefan Bloodworth on his grandfather's farm.

SPECIMEN CITATION: U.S.A. North Carolina: Durham Co., straggly shrublet 2–3 dm tall growing in a thicket or low woods on ridge top of the Jordan Farm perhaps 1.5 miles NE of Bahama and 2 miles along Wilkins Road (State Rd 1613) overlooking the Flat River several hundred feet below, 6 Apr 2003, *R.L. Wilbur, S. Bloodworth & E.M. Wilbur 76411* (DUKE).

Gaylussacia brachycera is now known from eight states (Del., Pa., Md., Va., N.C., W.Va., Ky., and Tenn.; Figure 1). It was mistakenly reported from the inner coastal plain of South Carolina (Radford et al.

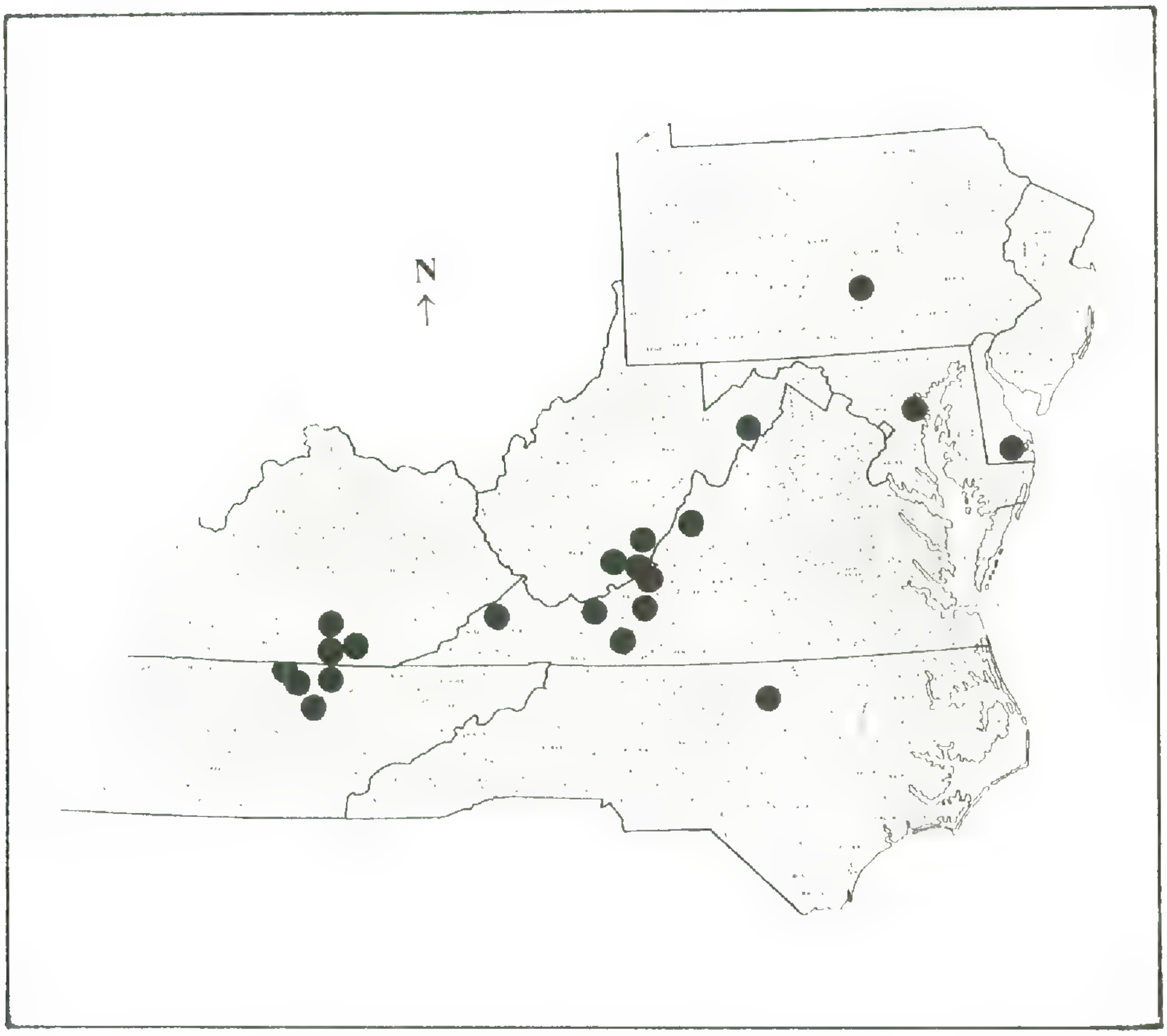

Figure 1. Distribution of *Gaylussacia brachycera*, based on specimens examined from 24 herbaria.

1968), but this has been shown to be a misidentification of a blueberry of the genus *Vaccinium* section *Herpothammus* (Small) Sleumer (Kirkman and Ballington 1990; Kirkman et al. 1989; Rayner and Henderson 1980; Uttal 1986). As a *Vaccinium*, it has been ranked as a species (Rayner and Henderson 1980; Uttal 1986), a subspecies (Kirkman and Ballington 1990), and as a minor variant unworthy of formal recognition from the far more widespread *V. crassifolium* Andr. (Luteyn et al. 1996).

The late Professor Edgar Wherry (1934) offered sound advice seventy years ago in suggesting that "before theorizing as to the principles of plant distribution, . . . let us first find out more as to where our species of native plants really grow." The plant that stimulated that bit of sage advice was *Gaylussacia brachycera* (Michx.) A. Gray, first described by Michaux (1803) as *Vaccinium brachycerum* from what is now either western Virginia or eastern West Virginia. Shortly thereafter, Matthias Kinn made a collection of the same species in what is now Greenbrier County, eastern West Virginia. After these two discoveries, the species

disappeared from scientific view for more than 45 years. Even Asa Gray was unable to secure a specimen for illustration until Professor Spencer F. Baird, then of Dickinson College, discovered the plant in nearby Perry County, Pennsylvania.

From Baird's collection, Asa Gray (1846) was able to prepare a fuller description, leading to the transfer of the species with 10 pyrenes to *Gaylussacia* Kunth, a largely South American genus, under which name it and the other North American huckleberries were grouped for nearly nine decades (e.g., Camp 1935, 1941; Gray 1886; Robinson and Fernald 1908; Small 1897). However, Small (1933) concluded that the perhaps nine or so taxa then assigned to the genus *Gaylussacia* and found in the eastern United States were better segregated into three genera, which he felt were clearly distinguished from their supposed South American congeners. Small placed the box huckleberry in the monotypic genus *Buxella*, which turned out to be a latter homonym of a generic name that van Tiegham had earlier proposed for a genus of the Buxaceae from Madagascar and South Africa. Small's nomenclatural error has never been corrected, but his taxonomic judgment that the box huckleberry was deserving of independent generic recognition has received at least minimal support from Camp (1940) and more recently from the largely molecular investigation of Floyd (2002). Neither felt the evidence was conclusive, but both noted that the box huckleberry was so isolated from its supposed congeners that its relationships clearly deserved further investigation.

After surveying the historic record of the box huckleberry and the meager representation in some of the larger herbaria and observing only the largest colony of the species in Pennsylvania, Coville (1919) pessimistically concluded that this rare and beautiful shrub was nearing extinction. Coville found that hearsay reports of the presence of the species were not substantiated by vouchers of their occurrence except for the stations in Pennsylvania and Delaware, and the latter station appeared at that time no longer to exist. No doubt stimulated by Coville's discouraging account, Wherry re-located the site in southern Delaware in early 1919.

The Reverend Fred W. Gray (1922) altered the above gloomy picture by spectacularly demonstrating the effectiveness of enlisting the natives of rural, eastern West Virginia. He sent letters to individuals and to the small newspapers of the region requesting information about the source of the berries used in making "juniper pie." As a result of Gray's letter writing and newspaper inquiries, he was soon swamped by reports of 75 or so stations for the berries. Gray soon verified 40 or so of the stations in Greenbrier, Monroe, and Summers Counties, West Virginia, with

unchecked reports from the Pocahontas and Raleigh Counties in West Virginia, and additional reports from bordering counties in Virginia. The abundance of stations in the area seemed to have reassured all concerned that the box huckleberry was definitely not on the verge of extinction. Unfortunately, Gray published no further reports on the remaining locations sent to him. [It should be noted here that interest in the economic possibilities of the box huckleberry was not only in the quality of its fruit but also in its foliage, which made it "the most beautiful native evergreen ground cover known" to Harlan P. Kelsey, then a well-known landscape designer (Coville 1919).]

Tantalizing bits of information suggest that the colonies, or at least the two that were best known and most completely surveyed by biologists, were each a single plant spread by vegetative growth from a single seed. This suggested to Coville (1919) that the largest colony (an eight-acre patch in Pennsylvania) was 1200 years old, allowing for an average six inches of growth per year. Although the plants were in fruit at the time of Coville's visit, no seedlings were in evidence, and every tuft of new foliage investigated as a possible new seedling was found to be attached to a rootstock leading to an older plant. A native of the area stated that the colony fruited every year, but seedlings were unknown. Coville speculated that the colony was completely or largely self-incompatible. Fruit was set, but the seeds either did not germinate or yielded only a very few seedlings incapable of surviving competition. Coville planted 1600 seeds gathered from the Pennsylvania population. These yielded only three unthrifty seedlings. This certainly suggests that the colony was effectively self-sterile. Plants from the Pennsylvania colony were crossed with those from the Delaware patch; the resultant fruit was developing but had not yet matured when Coville's article was submitted for publication. Wherry (1934) belatedly provided the only information available as to the results of the cross between the Delaware and Pennsylvania colonies: that cross resulted in four seeds that germinated into "vigorous seedlings," just as Coville had predicted might be the case. Clearly, though, the economic possibilities of the box huckleberry as either an esteemed fruit or as a foliage ground cover are yet to be realized.

It has been suggested that *Gaylussacia brachycera* is a very recent bird-dispersed introduction into the Durham, North Carolina area. The size of the Durham colony is approximately 125 × 100 feet, and its location on a remote dry ridge above the Flat River, together with what little is known about the reproductive biology of the species, argues against a recent avian introduction, and suggests instead a long presence

in its current location. Figure 1 shows the counties from which the box huckleberry was represented in the 24 herbaria from which specimens were examined about a decade ago. The map illustrates that the range of the species is considerable, as are the gaps between known populations. Although it is true that the vagility of the box huckleberry is unknown, it would seem to be slight since its current range consists for the most part of widely scattered, isolated colonies. Field exploration for additional populations of *G. brachycera* and study of its reproductive biology would seem to be a most worthy task in which professional systematists, established herbaria, and amateur naturalists could most profitably and pleasurably collaborate.

I conclude these notes by listing the formal synonymy of the box huckleberry.

Gaylussacia brachycera (Michx.) A. Gray, Mem. Amer. Acad. Arts n.s. 3: 54. 1846.

Vaccinium brachycerum Michx., Fl. Bor.-Amer. 1: 234. 1803.
Vaccinium buxifolium Salisbury, Parad. Lond. Pl. 4. 1805. *nom. illegit.* (Article 52).
Adnaria brachycera (Michx.) Kuntze, Revis. Gen. Pl. 2: 383. 1891.
Decamerium brachycerum (Michx.) Ashe, Rhodora 33: 197. 1931.
Buxella brachycera (Michx.) Small, Man. S.E. Fl. 1009, 1506. 1933.

REPRESENTATIVE SPECIMENS: U.S.A. Delaware: Sussex Co., shores of Indian River, near Millsboro, May 1870, *W.M. Canby s.n.* (A, GH, PH); sandy banks, S side of Indian River, 1 mi below Millsboro, 23 May 1875, *A. Commons s.n.* (GH, NY, PH, US). Kentucky: McCreary Co., in upland pinewoods, mostly along ridge crests, near Peter's Lookout Tower, 28 Jun 1978, *S.W. Leonard 7178* (FSU, VDB); Pulaski Co., Beaver Creek area between Alpine and Greenwood, 11 Sep 1940, *F.T. McFarland, 1st Century Fl. Kentucky 35* (DUKE, GH). Maryland: Anne Arundel Co., 1 mi E of Pasadena, steep bank of Magothy River under *Kalmia latifolia*, 25 May 1950, *F.H. Sargent s.n.* (FLAS, FSU, NCSC, WVA). North Carolina: Durham Co., low woods on ridge top perhaps 1.5 mi NE of Bahama and 2 mi along State Rd 1613 overlooking the Flat River, 6 Apr 2003, *R.L. Wilbur, S. Bloodworth & E.M. Wilbur 76411* (DUKE). Pennsylvania: Perry Co., hills near New Bloomfield, 19 May 1869, *T.C. Porter s.n.* (GH, NCSC, NY); hillsides near New Bloomfield, 19 Aug 1919, *J.K. Small s.n.* (FLAS, GH, MICH, NY, PENN, US, WVA). Tennessee: Fentress Co., light sandy soil, 15 May 1931, *H.M. Jennison et al., Pl. Exsiccatae Grayanae 577* (GH, DUKE, MICH, NCSC, PH, US, USF, WVA); Morgan Co., Clear Fork of S Cumberland River, Rugby, 31 May 1973, *H.M. Jennison et al. 1193* (DUKE, GH); Pickett Co., sandy oak-pine woods about 15 mi N of S entrance to Pickett State Park, 5 May 1973, *R. Kral 49854* (MICH, NCSC, TENN, VDB); Scott Co., South Fork National River . . . just E of Station Camp Creek, 2 Jun 1988, *B.E. Wofford 88-3* (GH, NY, TENN, US). Virginia: Bland Co., lower slope of Little Walker Mountain, about ½ mi W of VA 601, 8 Jan 1967, *A. Crooks 670* (FLAS, GA, NY, PH, TENN, VDB,

VPI); Carroll Co., N facing slope, quartz-feldspar pebble, Fries Junction, 13 Jun 1921, *H.W. Trudell s.n.* (DUKE, WVA); Dickinson Co., Pine Mountain S of Upper Skeg Fork headwaters, 24 Aug 1982, *T.F. Wieboldt 4453* (USF, VPI, WILLI); Montgomery Co., Prices Mountain near Blacksburg, 1930, *E.C. Magill s.n.* (VPI). West Virginia: Greenbrier Co., moist N hillside, Caldwell, 8 May 1934, *H. Gray 65* (TENN); Hardy Co., Buck Mountain, spur between forks of Ellis Hollow 2.75 mi SE of Baker, 26 Jan 1980, *T.F. Wieboldt & R.B. Davenport 3605* (USF, VPI, WILLI); Monroe Co., loamy soil under *Rhododendron* and *Kalmia* about 3 mi N of Hollywood, 28 Apr 1961, *M.G. Henry 7276* (DUKE, PH); acid bluff on Second Creek, 2 Jul 1941, *Southern Appalachian Bot. Club 248* (GH, FSU, NY, PENN, TENN, VDB, VPI, WVA); Pocahontas Co., Cass, 1926, *F. Gray s.n.* (WVA); Summers Co., second growth woodland . . . 0.2 mi along County Rd. 12 S of Hinton, 13 Aug 1966, *A. Crooks 480* (FLAS, PH, TENN, VDB, VPI, WILLI).

ACKNOWLEDGMENTS. We are most grateful to the staffs of the herbaria that loaned their specimens of North American species of *Gaylussacia* for examination: A, CHRB, CLEMS, DUKE, FLAS, FSU, GA, GH, MICH, NCSC, NCU, NEBC, PENN, PH, TENN, UNCC, US, USCH, USF, VDB, VPI, WCUH, WILLI, WNC.

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BOOK REVIEW

A Primer of Ecological Statistics by Nicholas J. Gotelli and Aaron M. Ellison. 2004. xviii + 510 pp. 103 illus. ISBN 0-87893-269-3 $34.95 (paperbound). Sinauer Assiocates, Inc., Sunderland, MA.

In the Preface, the authors state that their goal was to provide a single text that met the needs of ecologists and environmental scientists by providing a general introduction to probability theory, statistical inference, and hypothesis testing, plus a detailed discussion of experimental design and analyses typically encountered in ecological studies. It is intended to be "read and used, perhaps as a supplement to a more traditional text, or as a stand-alone text for students who have had at least a minimal introduction to statistics" and the authors hope that it will "find a place on the shelf (or floor) of environmental professionals who need to use and interpret statistics daily but who may not have had formal training in statistics."

The book is divided into three parts. Part I includes chapters on probability theory, random variables, probability distributions, summary statistics, framing and testing hypotheses, and a comparison of three "frameworks" for statistical analyses. Part II is devoted primarily to designing field studies and includes a fairly comprehensive set of experimental designs common to ecological research. It also includes a chapter on "Managing and Curating Data." Part III deals with the nuts and bolts of statistical analyses and includes chapters on regression, analysis of variance, analysis of categorical data (i.e., contingency tables) and multivariate analysis. The Appendix includes a section on "Matrix Algebra for Ecologists" plus a glossary that includes chapter references. The book is generously footnoted with a variety of explanatory and historical information. Figures are clear and include legends that are meant to be readable without reference to the text.

The authors acknowledge that while the term "primer" might suggest a short, simply explained introduction to the subject, the book is not short (510 pp.), nor is all of the covered material simple. The chapters are intended to stand alone and if you are looking for an easily readable section to warm up on, you might rather start with Part II, especially if you are less than fond of mathematical notation. If you choose to start with Part I, Chapter 1 jumps right into the mathematics of probability, incorporating set theory, set notation, Venn diagrams, and a number of definitions. The chapter concludes with a section on Bayes' Theorem explained primarily using Bayes' Formula. Much of the mathematic

notation in the chapter is not used extensively throughout the book. Considering the intended audience and in the spirit of a "primer," the material might better have been covered conceptually. If you are looking for more of a "how-to" approach to ecological statistics, you can safely skip most of this chapter. Chapter 2 introduces the idea of random variables and develops, conceptually and mathematically, the binomial, Poisson, and normal probability distributions. While these three distributions are the underpinnings of many statistical methods, the F-distribution and Chi^2 distributions, which are used extensively in the remainder of the book, are not covered. The chapter ends with an explanation of the Central Limit Theorem, "a cornerstone of probability and statistical analysis," but is missing an introduction to the distribution of sample means and its relationship to a population distribution. Chapter 3 is a fairly conventional treatment of measures of central tendency (arithmetic mean, mode, median, geometric mean) and dispersion (variance, standard deviation, standard error). The explanation of degrees of freedom is better than in most introductory texts and the discussion of skewness and kurtosis is excellent. Some less familiar statistics such as coefficient of dispersion are covered as well. There is a good discussion on when to use which statistic. Confidence intervals are covered with a clear explanation of what they mean, plus a comparison with credibility intervals used in Bayesian statistics. Chapter 4 is a formal discussion of the scientific method, deductive and inductive reasoning, and hypothesis development and testing. Helpful distinctions are made between statistical hypotheses and scientific hypotheses. Interpretation of *p*-values, the concepts of Type I and Type II errors, and statistical power are presented well. The chapter devotes several pages to the distinction between Bayesian Inference and Hypothetico-Deductive Methods which is interesting, but not essential to an understanding of the remainder of the book. The final chapter in Part I, titled "Three Frameworks for Statistical Analysis," works through a single sample problem using familiar parametric analysis (ANOVA in this case), Monte Carlo analysis, and Bayesian analysis. Similar comparisons are made in less detail later in the book. While the designs and analyses in Parts II and III are based primarily on parametric ("frequentist") methods, the book does a good job of exposing the reader to the concepts of Monte Carlo and Bayesian methods, which have become more prevalent with the availability of faster computers.

Part II, Designing Experiments, is by far the most readable part of the book. It is written in a more advisory style. This part alone may justify purchasing the book. Chapter 6 examines design considerations relevant

to ecological studies. It contrasts manipulative versus natural experiments, snapshot versus trajectory studies, and press versus pulse treatments. The authors make suggestions on replication including their "rule of 10" and tradeoffs with their "rule of 5." Chapter 7 is a collection of experimental and sampling designs that is initially broken down by the variable types (categorical versus continuous) of the independent and dependent variables. It differs from chapters in other Biostatistics books in that the mechanics of the analyses associated with each design are reserved for Part III. This makes the chapter readable and the concepts clear. General considerations are included for regression, ANOVA, logistic regression, and contingency table analysis. Designs discussed include one-way, RCB, nested, factorial, split-plot, and repeated measures designs. Special considerations for competitive experiments are discussed including additive, substitutive, and response surface approaches. Before-After, Control-Impact (BACI) designs are described for environmental impact studies. The authors suggest that in some cases, ANOVA may be an "intellectual straightjacket" causing scientists to neglect other useful designs. They suggest several Experimental Regression designs as preferable for certain applications. There is a general discussion of tabular designs and contingency tables. Chapter 8 provides useful general advice on managing and curating data. Much of this is common sense, but they make a strong case for keeping your data in good order. They stress the importance of transcribing field and lab data into spreadsheets immediately, constructing meta-data files to record critical information about the data (who, when, where it was collected, etc.). There is a section in the chapter on handling "outliers" in data sets, and some good ideas on using graphical exploratory data analysis for outlier detection. Data transformations are covered in this chapter as well.

Part III, Data Analysis, covers the mechanics of statistical analysis along with the underlying assumptions. Analyses are exemplified with data from some of the authors' studies. Chapter 9 is devoted to regression analysis. It starts with simple linear regression and provides a conceptual introduction plus methods and formulas for fitting the least-square regression line and calculating sums of squares and an F-ratio for hypothesis testing. There is a thorough section on confidence bands and prediction bands, plus an outstanding section on residual analysis. Conceptual coverage of Monte Carlo and Bayesian regression analyses is included. Cursory introductions to robust regression, logistic regression, multiple regression, and path analysis are included. Model selection methods for multiple regressions are covered including forward selection,

backward elimination, and stepwise methods. Chapter 10 covers ANOVA computational methods for the designs covered in Part II, Chapter 7. Although in practice these calculations are generally done using commercial statistical software, the authors stress the importance of understanding how the analyses work. For many designs, the default setting in statistical packages will not produce the correct analysis. This is especially true for some nested designs, split-plots, and mixed models including a combination of fixed and random treatments. There is a lot of information in this chapter but a few complete examples of some of the more complex designs would be helpful. Planned comparisons (orthogonal contrasts) and multiple comparison tests (Tukey's HSD) for pairwise and groupwise testing of means are explained well, although a number of alternative *a posteriori* tests are not covered. There is a spirited discussion in which the authors argue convincingly against the use of Bonferroni and Dunn-Sidak corrections for multiple analyses within a study. Advice is given on representing ANOVA and multiple comparison results for publication. It is not certain that the authors' suggestion to plot interaction between categorical treatments as line graphs will be universally embraced by journal editors. Most of us were taught that connecting means with a line implies a continuous treatment variable. Chapter 11 is devoted primarily to the analysis of counts and categorical data that are normally represented in contingency tables. Tests covered include Chi^2 Test of Independence, the G-Test, and Fisher's Exact Test. Criteria for when to use each test are discussed. Methods are supplied for calculating expected values for multi-way tables. Conceptual explanations for analyzing tables via Monte Carlo and Bayesian methods are given. A Goodness of Fit test is demonstrated using the fairness of a tossed Belgian Euro as an example. The Kolmogorov-Smirnov Goodness of Fit Test is demonstrated for testing for normality (or any other defined distribution). Chapter 12 provides an introduction to multivariate statistics. Explanations rely heavily on matrix algebra, and for those who need a refresher course in basic matrix operations, it is included in the Appendix. The chapter starts with Hotelling's T^2 Test, which is the multivariate equivalent of a T-Test. The authors walk the reader through a MANOVA, including calculations of common associated test statistics: Wilke's Lambda, Pillai's Trace, Hotelling-Lawley Trace, and Roy's Greatest Root. A short discussion of multiple comparisons is included. Ordination via PCA (Principal Components Analysis) is illustrated using one of the author's Cobra Lily morphological data sets. Factor Analysis, Principal Coordinate Analysis (PCoA), Correspondence Analysis (CA), and Multi-Dimensional Scaling are

briefly covered and guidance is given on how to choose between them. Where the goal of Ordination is to separate observations along the fewest axes, the goal of Classification is to group similar objects into identifiable groups that can be distinguished from neighboring classes. Agglomerative and divisive Cluster Analyses are compared. Hierarchical and non-hierarchical methods are discussed with K-Means analysis as an example of the latter. The section on Discriminant Analysis is good, but the snail data set used was not especially well suited. Two types of Multivariate Multiple Regression are discussed that are appropriate for examining associations between multivariate biological data and environmental data. Canonical Correspondence Analysis (CCA) is briefly explained, while Redundancy Analysis (RDA) is demonstrated using the less than ideal snail data set.

Overall, the book achieves the goals of the authors. It is a useful volume for graduate students and scientists involved in ecological field research. Part II is recommended for anyone planning a field study. Part III provides good explanations of statistical analyses that are regularly encountered in ecological work and journal articles.

—Christopher D. Neefus, Department of Plant Biology and Office of Biometrics, University of New Hampshire, Spaulding Hall, 38 College Rd., Durham, NH 03824.

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NEW BOOKS

A Dictionary of Plant Sciences edited by Michael Allaby. 2004 (reissue). 528 pp. illus. 51 line drawings. ISBN 0-19-860876-4 $16.95 (softcover). Oxford University Press, New York.

Flowering Plants of the Neotropics edited by Nathan P. Smith, Scott A. Mori, Andrew Henderson, Dennis Wm. Stevenson, and Scott V. Heald. 2004. 616 pp. illus. 307 color photos; 258 line drawings. ISBN 0-691-11694-6 $75.00 (hardcover). Princeton University Press, Princeton, NJ.

Jefferson's Garden by Peter Loewer. 2004. xii + 260 pp. ISBN 0-8117-0076-3 $21.95 (hardcover). Stackpole Books, Mechanicsburg, PA.

Mineral Nutrition of Plants: Principles and Perspectives, Second Edition by Emanuel Epstein and Arnold J. Bloom. 2005. xiv + 400 pp. illus. ISBN 0-87893-172-4 $79.95 (hardcover). Sinauer Associates, Inc., Sunderland, MA.

Working Forests in the Neotropics: Conservation through Sustainable Management edited by Daniel J. Zarin, Janaki R. Alavalapati, and Frances E. Putz. 2004. 416 pp. illus. ISBN 0-231-12906-8 $74.50 (hardcover). Columbia University Press, New York.

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NEBC MEETING NEWS

September 2004. Garrett Crow began with a slide show to preview the Saturday morning salt marsh field trip, followed by photos meant to interest the crowd in his July 2005 trip to the Amazon in connection with the New York Botanical Garden. He then introduced the evening speaker, Dr. Christopher Neefus from the University of New Hampshire, who spoke about "Living on the edge: Acclimation and adaptation of an intertidal seaweed."

Chris began his talk with a photo of Louis H. Sullivan, who designed office buildings during the late 19th and early 20th centuries. Louis, who often added beautiful botanical ornamentation to the facades of his buildings, was considered the father of the modern skyscraper, and was mentor to the famous architect Frank Lloyd Wright. More importantly, as Chris pointed out, he is credited with coming up with the concept of "form follows function," which Chris noted was an apt description of the evolution of intertidal seaweeds.

In the 1980s, Littler and Littler proposed a model of functional form for seaweeds, hypothesizing that physiological functions could be predicted via the seaweeds' morphological forms. Based on this model, there are six groups of seaweeds: Sheet, Filamentous, Coarsely Branched, Thick Leathery, Jointed Calcareous, and Crustose. In the shallow subtidal zone, the Thick Leathery group is well represented—the species found there tend to be tough, rubbery, and thick. These seaweeds have adapted to deal with the mechanical stress caused by wave action, and can tolerate changes in temperature, reducing enzymatic reactions when it is too hot or cold.

In the intertidal zone, seaweeds are submerged in ocean waters for only part of each tidal cycle, and as a result have had to evolve to tolerate an extreme range of temperatures, from −20°C to 40°C. When exposed to the air, they may also have to deal with high light levels and strong ultraviolet radiation. Mechanical stress can be as high here as in the subtidal zone, but decreases with increasing elevation. Competition from other seaweeds and herbivory also decrease as elevation increases. Common species found in the intertidal zone include *Ascophyllum nodosum* and *Fucus vesiculosus*, both from the Thick Leathery group.

In the highest part of the intertidal zone, the environment is often too extreme for the adaptations described above. One species found there is *Porphyra linearis*, a winter annual. This seaweed is an alga from the Sheet group that grows in thin layers on the tops of rocks. Having a life cycle that is restricted to winter and spring allows *P. linearis* to avoid the

highest temperatures of the season. When exposed to air at low temperatures, this species freezes to the rocks, but is able to recover. Perhaps even more amazing, *P. umbilicalis* and *P. rediviva* respond to extreme heat by drying out completely, and can resume growth when they are rehydrated. Chris noted that there have been some amazing observations of *Porphyra* growth following the rehydration of dried herbarium specimens!

Since these species live so high up in the intertidal zone, they may be submerged for less than one hour each day, meaning they only have a short amount of time to acquire nutrients. In response, some *Porphyra* species have adapted to have the greatest rate of nutrient uptake within the first hour of exposure to a nutrient source. These nutrients can be stored within the seaweeds as phycobilin-protein pigments that also serve as accessory photosynthetic pigments.

To deal with interspecies competition, some *Porphyra* species have adapted to grow epiphytically on organisms such as barnacles, or even on other seaweeds including *Fucus* species. The moist tissue of the *Fucus* helps hydrate the *Porphyra*, extending the time the plant can photosynthesize. Chris went on to describe other adaptations of seaweed morphology to the harsh environment of the intertidal zone. Species with linear and lanceolate forms have low drag, allowing them to handle high levels of mechanical stress. These species may be "wave-pruned," but are fast growing and recover quickly by virtue of their form—they tend to be composed mainly of undifferentiated tissue, meaning there is little impact to the plant if part of it is torn away. Chris ended the talk by noting what may be the most important function of *Porphyra*—its form made it ideal to use as a wrapper for sushi.

—Jennifer Forman Orth, Recording Secretary.

September Field Trips. On Friday afternoon, September 10, Drs. Chris Neefus and Art Mathieson of the University of New Hampshire (UNH) led a party of approximately ten Club members and several UNH students to explore the seaweed flora of the rocky intertidal zone of Wallis Sands in Rye, New Hampshire, and the salt marsh of Brave Boat Harbor in Kittery, Maine. The rocky intertidal zone of Wallis Sands is a very exposed and disturbed environment, with high wave action and sand scour. The group scrambled down to the shoreline to observe the thick layer of wrack that had washed ashore. Several species were identified, with some noteworthy field characteristics. *Laminaria saccharina* (sugar kelp) is large and ribbon-like, with a very thick and strong

holdfast. Somewhat smaller, *Laminaria digitata* (kelp) has "digits" along the margin. Although not a true kelp, *Agarum* sp. (shotgun kelp) could be identified by the numerous holes in the thallus. *Phycodrys rubens* (sea oak) is one cell thick except along the midrib. Green, threadlike, tangled balls of *Chaetomorpha* sp. were scattered about; *Desmarestia* sp. exudes sulfuric acid, and has minute spikelets on the margin. *Ulva* sp. (sea lettuce) could be discerned by its flat, bright green thallus.

A few low intertidal species were observed, including *Fucus spiralis*, *Chondrus crispus* (Irish moss), *Corallina*, and *Ascophyllum nodosum* (rockweed), which covered much of the rock surfaces of the intertidal zone. In the high intertidal *Porphyra umbilicalis* (nori) grew attached to rocks. This economically important seaweed is used in making sushi wraps. *Porphyra* was observed with variable pigmentation, from purple to green. The light-harvesting pigment phycoerythrin gives the thallus its purple coloration. The level of pigment depends on the light level. Plants growing in shaded areas are dark purple, while those exposed to full sunlight appear greenish. Pigmentation is also controlled by the amount of nutrient availability; a decrease in pigmentation may be associated with low nutrients.

For the second part of the field trip, Art Mathieson first described the habitat, morphology, and phenotypic variation of two seaweed species, *Ascophyllum nodosum* and *Fucus vesiculosus*. The group then journeyed through deciduous forests down to Brave Boat Harbor to search among *Spartina patens* for the seaweed. The Brave Boat Harbor salt marsh has a well-drained, sandy substrate and is highly susceptible to erosion. Art taught the group how to distinguish between ecads and germlings. The former is a phenotypic variant of a species and is caused by extensive proliferation and degeneration of detached fragments. Germlings could be discerned by the presence of a distinct, discoid holdfast. Several phenotypic variants were found, including *Ascophyllum nodosum* ecad *scorpioides*, *Fucus vesiculosus* ecad *volubilis*, and *Fucus cottonii*.

On Saturday morning, September 11, Dr. Garrett Crow of UNH, accompanied by his phytogeography class, led several Club members to explore the vascular flora of the salt marshes and sand dunes along the New Hampshire coastline. The first stop was to a salt marsh in Rye, just south of Odiorne State Park. Here, the group trekked through pure stands of *Spartina patens*, *Distichlis spicata*, and *Juncus gerardii*. Other species encountered in the salt marsh included *Atriplex subspicata*, dense red patches of *Salicornia europaea*, *Spartina alterniflora*, *Solidago sempervirens*, *Potentilla anserina*, *Triglochin maritima*, *Limonium carolinianum*, *Suaeda maritima*, *Plantago maritima*, and *Scirpus*

robustus. In some of the pools, *Ruppia maritima* was found. Garrett discussed the geographic distribution of several species, the role of environmental factors in shaping this type of plant community, and adaptations of species to such conditions.

The group then met at the Seabrook sand dunes. This area represents the largest coastal sand dune remnant in the state of New Hampshire. Prior to protection of this community, the sand dunes suffered a substantial amount of disturbance from ATV (all-terrain vehicle) usage. Plants that colonize the dunes are adapted to strong prevailing winds, storm activity, shifting sands, salt spray, and high solar radiation. *Ammophila breviligulata* and *Lathyrus japonicus* are early colonizers of the foredune. Several species were observed among the dunes, including *Polygonella articulata*, *Lechea maritima*, *Cakile edentula*, *Artemisia stelleriana*, *A. caudata*, *Hypericum gentianoides*, and *Myrica pensylvanica*. *Prunus maritima* grew intermixed with *Toxicodendron radicans*, making the collection of its sweet and succulent fruit a risky endeavor. Because the sand dunes are a rare community in New Hampshire, this area is the location of several state-listed taxa, including *Aristida tuberculosa*, *Cyperus grayi*, and *Hudsonia tomentosa*, all of which the group observed. Sunken forests, hollows among the dunes where the establishment of shrubs is followed by tree species, were scattered among the dunes. A few members of the group followed Garrett into one of them. The sunken forest was cooler, being densely shaded by a canopy of *Acer rubrum*, *Populus tremuloides*, and *Pinus rigida*. Shrub species included *Ilex verticillata*, *Amelanchier stolonifera*, *Vaccinium* sp., and *Viburnum* sp. The forest floor was colonized by species such as *Parthenocissus quinquefolia*, *Aralia nudicaulis*, *Trientalis borealis*, *Maianthemum canadense*, and *Carex pensylvanica*.

—Mare Nazaire, Recording Secretary *pro tempore*.

October 2004. The New England Botanical Club celebrated its 1000th meeting since its original organization at the Massachusetts Audubon Society's Broadmoor Wildlife Sanctuary in Natick. Members and guests enjoyed hors d'oeuvres and displays of botanical art by club members Erika Sonder and Anita Sebastian, while a slide show of images and documents from the NEBC archives was displayed on a large screen. After a catered buffet, President Art Gilman welcomed everyone and spoke briefly about the many great "Away" meetings the club has had in and around New England over the past few years. He noted that the club currently has more than 400 members; they and 350 institutions subscribe to *Rhodora*.

Past President Lisa Standley introduced the evening's speaker, Dr. David Barrington from the University of Vermont. The club has had the honor of hearing Dave speak on several occasions over the years. For the thousandth meeting of a club that spends most of its time asking why plants grow where they do, his talk was appropriately titled "The Big Thaw: New England Flora in the Holocene."

Dave began his talk by noting that the mountaintops of New England had captured the fascination of many of the first NEBC members. Ausable Chasm in New York serves as one striking lesson in the effects of time and change on flora and fauna. A deep and narrow divide almost a mile long, it was originally thought to have been formed in the Oligocene era, but actually developed during the last 10,000 years.

In 1846, a beluga whale was unearthed during the construction of a railroad in Vermont. The presence of such a creature, referred to as the "Charlotte Whale" after the town near where it was discovered, supports the idea that there was once an arm of the ocean in the Champlain Valley. While studying flora from the Pleistocene glaciation, E. C. Pielou concluded that at maximum glaciation (18,000 years ago), ice covered much of the terrain. However, during this ice age a series of large sandy islands was exposed along the northeast coast. Lake Champlain was indeed at one time an arm of a giant sea whose land was compressed by the huge weight of ice.

Dave described the work of Norton Miller, who has studied the recovering New England flora of 12,000 to 13,000 years ago, specifically looking at when and where species were found. This work uses both pollen cores and macrofossils. The portions of a species' range where the highest genetic diversity is found are thought to be those where populations have been around the longest, especially those that survived through the ice age in what are termed "refugia." For example, when looking at *Fagus sylvatica* in Europe, scientists found that genetic diversity in this species is highest in the southernmost part of its range. This is hypothesized to be because subsets of the southern populations were able to "hide out" in refugia through the ice age. Another example of this pattern is *Asclepias exaltata*, an eastern North American milkweed species that is very common in the South. In the North, it is rare and has low genetic variation as well.

Saxifraga oppositifolia is found at Smugglers Notch in Vermont on wet cliffs; the southern limit of its distribution is currently in New England. A group headed by Dr. Abbott did a genetic study of this species, which was found to have spent the height of the Pleistocene era on exposed land in Siberia, where the highest genetic diversity is now found. The species

then repopulated the Arctic through North America and through Eurasia. *Dryas integrifolia* is another Arctic species for which a set of refugia can be hypothesized from genetic data. There are many records of the pollen of this species as well as fossils in refugia, with two centers of diversity being the high Arctic and Beringia.

Dave then described the thesis research of Pete Walker, a University of Vermont graduate who worked with Cathy Paris. Pete studied *Ammophila breviligulata* (beach grass), which is widely distributed along the Atlantic coast and Great Lakes regions. However, plants found along Lake Champlain have been labeled as *A. champlainensis*. There has been some question as to whether this was a "true" species, though the Lake Champlain plants flower in a different month. Pete determined that the Great Lakes populations were actually morphologically intermediate between the North Atlantic and Lake Champlain populations. It is likely that the Lake Champlain plants arrived with the ancient Champlain Sea and diverged from other populations since the salt waters receded 10,000 years ago. The North Atlantic populations have the highest genetic diversity, likely because there was plenty of exposed sand on the coast during the Pleistocene, providing a refugium. *Lathyrus japonicus*, often a companion of beach grass, grows on both the Atlantic and Pacific coasts of North America. An isozyme study showed that Pacific alleles were most common in the north and dwindled in the south, while Atlantic alleles were found only in the Atlantic populations, suggesting that there are actually two endemic centers for this species.

Dave spent the last part of his talk discussing several other interesting case studies of plant species that survived the Pleistocene era in refugia, including *Adiantum pedatum*. He mentioned *Hudsonia* as a candidate for future study of glacial refugia and Holocene migration. He then took several enthusiastic questions from the audience. The Club finished the 1000th meeting celebration with an excellent dessert table and a sparkling cider toast.

—Jennifer Forman Orth, Recording Secretary.

REVIEWERS OF MANUSCRIPTS

2003–2004

The Editor-in-Chief of *Rhodora* is grateful to the members of the editorial staff and to each of the following specialists for their participation in the review process. Their conscientious evaluation of manuscripts helps to maintain the quality of this journal.

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THE NEW ENGLAND BOTANICAL CLUB
22 Divinity Avenue
Cambridge, MA 02138

The New England Botanical Club is a nonprofit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, and has a large herbarium of New England plants and a library. It publishes a quarterly journal, RHODORA, which is now in its 106th year and contains about 400 pages per volume. Visit our web site at http://www.huh.harvard.edu/nebc/

Membership is open to all persons interested in systematics and field botany. Annual dues are $45.00, including a subscription to RHODORA. Members living within about 200 miles of Boston receive notices of the Club meetings.

To join, please fill out this membership application and send with enclosed dues to the above address.

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